A PHYLOGENETIC ANALYSIS OF THE WHISTLING AND WHITE-BACKED DUCKS (ANATIDAE: DENDROCYGNINAE) USING MORPHOLOGICAL CHARACTERS

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ABSTRACT

A phylogenetic analysis of the eight species of whistling-duck (*Dendrocygna*) and the White-backed Duck (*Thalassornis leuconotus*) was performed using 68 characters of the skeleton, trachea, and natal and definitive integument. Three shortest trees were found, each having a length of 91 and a consistency index of 0.766 (excluding uninformative characters). Monophyly of *Dendrocygna* + *Thalassornis* was supported by three unambiguous synapomorphies, and monophyly of *Dendrocygna* by eight unambiguous synapomorphies. The three shortest trees supported two major clades within *Dendrocygna*, each supported by three synapomorphies: (1) *D. autumnalis* + *D. viduata*; and (2) the other six species of *Dendrocygna*. Within the latter, the three shortest trees defined two groups: (1) *D. guttata* + *D. arborea* (supported by three synapomorphies); and (2) an unresolved trichotomy (supported by one unambiguous synapomorphy) involving *D. eytoni*, *D. bicolor*, and the clade *D. arcuata* + *D. javanica* (the last two united by three synapomorphies). A majority-rule consensus tree of 1000 bootstrapped replicates confirmed all of the branches common to the three equally parsimonious trees. All species of *Dendrocygna* and (especially) *Thalassornis* were highly autapomorphic. Mapping of selected eco-morphological parameters on the trees revealed evolutionary patterns in body mass, egg mass, relative clutch mass, and diving habit, with lesser trends in preferred nest site, perching habit, and diel activity pattern. A phylogenetic classification of the group is presented and related systematic and biogeographic issues are discussed.

INTRODUCTION

The whistling or tree ducks of the genus *Dendrocygna* represent one of the most distinctive genera of the Anatidae; erect posture, relatively elongated necks and legs, and (in most species) conspicuous habit of perching in trees distinguish the members of the genus from most other waterfowl (Phillips, 1922; Delacour, 1954; Bolen and Rylander, 1983). Early taxonomists differed on whether the available anatomical evidence favored placement of the genus nearer the Anserinae or with the more typical ducks (Salvadori, 1895; Phillips, 1922; Peters, 1931), although a consensus supporting the former position was achieved by the middle of the twentieth century (Boetticher, 1942, 1952; Delacour and Mayr, 1945; Verheyen, 1953; Delacour, 1954; Woolfenden, 1961). Recent phylogenetic analyses using morphological characters corroborate the view that the group diverged from other Anatidae at least as early as the geese and swans (Anserinae), rendering the vernacular term "duck" of only descriptive utility in reference to the smaller (polyphyletic) members of the order Anseriformes (Livezey, 1986; Livezey and Martin, 1988). Phenetic patterns of molecular similarity also are consistent with an early divergence of the whistling-ducks (Jacob and Glaser, 1975; Brush, 1976; Jacob, 1982; Numachi et al., 1983; Scherer and Sontag, 1986; Madsen et al., 1988; Sibley et al., 1988; Sibley and Ahlquist, 1990).

Relationships within *Dendrocygna* have received substantial speculation but have not been subjected to phylogenetic analysis, resulting in the adoption of no

widely accepted groupings within the genus and varying sequences of species in published taxonomic arrangements (Salvadori, 1895; Phillips, 1922; Peters, 1931; Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1978). Delacour (1954: 29) concluded: "No completely satisfactory system can be devised for classifying the different species with their many and sometimes divergent features." Delacour (1954:30) also commented: "We have adopted different sequences in the past, and others have been proposed by various authors. Indeed, we must admit that almost any is equally acceptable." Johnsgard (1961*a*:fig. 1) depicted the only species-level diagram of "evolutionary relationships" among the species of *Dendrocygna*, a "tree" derived using no explicit inferential algorithm and based principally on similarities of behavior and natal plumage. Behavioral patterns described by Johnsgard (1961*a*) lacked polarities and the taxonomic groupings supported by some behaviors were only vaguely defined, but he proposed close relationships between the following groups of species of *Dendrocygna*: (1) *guttata* and *eytoni*; (2) *arborea* and *autumnalis,* in turn closely related to *viduata*; and (3) *bicolor* and *arcuata,* in turn linked to *javanica* (the last group being depicted in his figure 1 but apparently contradicted in text). These groupings evidently gave rise to a species sequence used in subsequent works by Johnsgard (1965, 1978, 1979), which apparently formed the basis for the subgeneric groupings given by Wolters (1976), and the species sequence was adopted by several other authors in descriptive and comparative works (Madge and Burn, 1988; Rohwer, 1988; Scott and Clutton-Brock, 1989; Sibley and Monroe, 1990; McNeil et al., 1992).

The White-backed Duck (*Thalassornis leuconotus*) traditionally was classified among the stiff-tailed ducks (Oxyurini), principally on superficial similarities related to specialization for diving (Peters, 1931; Boetticher, 1942, 1952; Delacour and Mayr, 1945; Delacour, 1959, 1964; Johnsgard, 1961*a*, 1965). Closer examination of behavioral and anatomical characters by Johnsgard (1967), Kear (1967), and Raikow (1971) revealed several primitive characters that *Thalassornis* shared with the geese, swans, and *Dendrocygna* that were lacking in the comparatively derived Oxyurini and other Anatinae. Johnsgard (1978:xviii) clarified his opinion on the position of *Thalassornis* by depicting it as the sister-group of *Dendrocygna* in an intuitive evolutionary tree. Johnsgard (1979) incorporated this view taxonomically through the inclusion of *Thalassornis* within the Dendrocygninae. The phylogenetic analysis by Livezey (1986) confirmed an early divergence of *Thalassornis* within the Anatidae and contradicted the inclusion of the genus among the Oxyurini. However, the phylogenetic analyses by Livezey (1986), Livezey and Martin, 1988, and Livezey (1989) failed to document a sister-group status of *Thalassornis* with *Dendrocygna,* and discovered several equally parsimonious relationships among *Thalassornis, Dendrocygna,* and the Anserinae. In addition, no support for a close relationship between *Dendrocygna* and *Coscoroba,* suggested by Delacour and Mayr (1945) and Delacour (1954), was found in the osteological study by Woolfenden (1961), the behavioral comparisons by Johnsgard (1961*a*, 1965), or the phylogenetic analyses by Livezey (1986, 1989) and Livezey and Martin (1988).

This paper describes a species-level phylogenetic analysis of the whistling-ducks and the enigmatic White-backed Duck based on characters of the skeleton, trachea, natal plumage, and definitive plumages and soft parts. The objectives of the phylogenetic analysis were to test the proposed monophyly of the genera *Dendrocygna* and *Thalassornis,* to resolve relationships among species of *Dendrocyg-*

na, and to examine evolutionary patterns in selected ecomorphological characteristics within the context of the inferred phylogenetic tree(s).

MATERIALS AND METHODS
Taxonomy

For purposes of analysis, I adopted the species-level taxonomy used by most twentieth-century systematists (e.g., Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1978, 1979) and recognized eight species of *Dendrocygna* and one species of *Thalassornis*. Geographic variation within species is minimal within these two genera (although variation evident in *D. viduata* may warrant further study), and subspecific taxa generally are recognized in only three species (Delacour, 1954; Madge and Burn, 1988). Three poorly differentiated subspecies of *Dendrocygna arcuata* are recognized on mensural grounds, listed in order of decreasing size: widespread *D. a. australis* (Australia and New Guinea), nominate *D. a. arcuata* (East Indies), and insular *D. a. pygmaea* (New Britain and formerly Fiji). Two subspecies of *D. autumnalis* are recognized on the basis of size and modest, possibly clinal differences in plumage coloration: northern and comparatively large *D. a. autumnalis* (Panama north to southern Texas), and southern and comparatively small *D. a. discolor* (Panama south to northern Argentina and Amazonian Peru). The latter differs from the nominate form in the presence of gray on the otherwise chestnut color of the mantle and lower breast. Finally, two subspecies of *Thalassornis leuconotus* are recognized: comparatively pale, slightly larger *T. l. leuconotus* of tropical continental Africa; and comparatively dark, coarsely marked, and slightly smaller *T. l. insularis* of Madagascar. Of these, only *Dendrocygna (autumnalis) discolor* even approached a level of qualitative differentiation to be considered specifically distinct for purposes of analysis, and this form was clearly monophyletic with the nominate form and therefore did not alter any phylogenetic inferences within the genus. Therefore questions concerning evolutionary units or "phylogenetic species" (Cracraft, 1983, 1988; McKitrick and Zink, 1988) were not of practical consequence in this analysis. In the text and proposed classification, hyphenation and capitalization of the English names of species follow the conventions of Parkes (1978).

Specimens

Plumage patterns of adults were compared using series of study skins in the collections of several major museums, most importantly the National Museum of Natural History and American Museum of Natural History. Colors of the irides, bill, tarsi, and feet of adults were characterized using published descriptions (e.g., Phillips, 1922; Delacour, 1954; Johnsgard, 1978; Madge and Burn, 1988), notes on specimen labels, and photographs of living individuals. Patterns of natal plumage were ascertained by comparisons of study skins and (rarely) fluid-preserved specimens of downy young. Skeletal specimens of adults, generally five or more specimens of each species, were included in osteological comparisons. Tracheal characters were confirmed using ossified elements in skeletal specimens (principally those in which the trachea remained intact) and complete tracheae removed from fluid-preserved specimens (some previously mounted and dried).

Definition of Characters

Definition of morphological characters was based on a survey of the literature on plumage pattern, skeletal and tracheal anatomy (Shufeldt, 1909, 1914; Phillips, 1922; Delacour, 1954, 1964; Johnsgard, 1961a, 1961b, 1962, 1965, 1967, 1978; Woolfenden, 1961; Humphrey and Clark, 1964; Raikow, 1971; Bolen and Rylander, 1974, 1983; Womack et al., 1977; Rylander et al., 1980; Madge and Burn, 1988; King, 1989; Marchant and Higgins, 1990; Hoyo et al., 1992; Nelson, 1993), as well as direct study of specimens. A total of 68 morphological characters were defined for this analysis: 13 characters of the skeleton, two of the trachea and syrinx, eight of the natal plumage, and 45 of the definitive plumage and soft parts (Appendix 1). Most skeletal characters were adapted from those described by Livezey (1986, 1989). Each character (identified by number) comprised two or more states (distinguished by letters), one of which was hypothesized as the primitive or plesiomorphic state based on outgroup comparisons (generally designated as "a"). These 68 characters, coded for each of the nine members of the ingroup and an "ancestral" vector (see below), produced a data matrix of dimension 9×68 (Appendix 2). Three of the 612 matrix entries were coded as missing or indeterminate because of unknown polarity (one, in the ancestral vector) or problematic comparability of states (two, within ingroup taxa). Eleven of 68 characters were "multistate," i.e., included two or more derived or

apomorphic states in addition to the single primitive state. Of these, only one character (character 19) was analyzed as ordered (i.e., a particular ordination of derived states was assumed). Autapomorphies, character changes that are unique to a single species, cannot contribute to the resolution of interspecific relationships (Wiley, 1981). However, autapomorphies were included in this analysis in order to quantify interspecific differentiation, because such phenetic differences traditionally have been accorded considerable weight in previous attempts at phylogenetic inference (e.g., Delacour, 1954; Johnsgard, 1961a, 1965, 1978) and such character divergence can be depicted in phylogenetic trees independently of inferred topologies and summary statistics.

Character Polarities and the Hypothetical Ancestor

Use of a hypothetical ancestor, a vector of primitive character states based on outgroup comparisons, was used to root the phylogenetic tree(s). This method provided a single, simple root for the ingroup without ancillary analytical digressions concerning relationships among outgroups in the present analysis, and was used in previous phylogenetic analyses of the order (Livezey, 1986, 1989; Livezey and Martin, 1988). The selection of outgroups studied in the determination of polarities was based on the intergeneric relationships inferred in earlier works (Livezey, 1986, 1989) and ongoing analyses of primitive Anseriformes (Anhimidae, Anseranatidae) and the geese and swans (Anserinae). Outgroups selected for comparisons were *Anseranas, Cereopsis, Anser, Branta,* and *Stictonetta.* Using the hypothetical ancestor, monophyly of the ingroup in the present analysis is supported if one or more unambiguous synapomorphies for the taxa exclusive of the hypothetical ancestor are discovered (i.e., if the basal branch has positive length). In addition, in a larger analysis (Livezey, in preparation) of the phylogenetic relationships of *Dendrocygna, Thalassornis,* all modern species of the Anserinae, and other subfamilies of Anatidae, the monophyly of *Dendrocygna + Thalassornis* is supported as the shortest topology. This contrasts with the poor resolution achieved in previous phylogenetic analyses of this part of the Anseriformes (Livezey, 1986, 1989; Livezey and Martin, 1988).

Derivation of Trees

Phylogenetic trees were derived from the character matrix by the criterion of parsimony (minimization of number of changes in character states necessitated by the tree), using the vector of inferred ancestral states as a root (Wiley, 1981). All characters were assigned unit weight. The character-state optimization used was accelerated transformation (option ACCTRAN); employment of delayed transformation (DELTRAN) did not affect the solution set. The shortest (most parsimonious) trees were found using the branch-and-bound algorithm of the software package PAUP 3.1 (Swofford, 1993), a method guaranteed to find the shortest tree(s) representative of a given character set and ancillary restrictions (rooting vector, ordering and weighting of characters). Several summary statistics (Swofford, 1993) were used to describe the inferred tree(s): tree length; consistency index, excluding uninformative characters; homoplasy index, excluding uninformative characters; retention index; and rescaled consistency index.

A bootstrapping procedure using the branch-and-bound method was employed to generate 1000 topological replications in which single characters were deleted from the analysis. Stability of branches within the final tree was summarized by a 50% majority-rule consensus tree of these 1000 replicate trees. The resultant consensus tree reflects comparatively well-supported or "robust" clades by depicting only those supported by one or more character changes (synapomorphies) in a majority of the 1000 bootstrapped replications; clades supported by only one synapomorphy in a majority of the replications were collapsed into the least-inclusive, adequately supported polytomies including those terminal lineages. Because of the distributional assumptions necessary in associated statistical inferences (Felsenstein, 1985; Sanderson, 1989), the bootstrapping procedure is intended to provide an index to the empirical support for the branches in the tree(s) and is not used for formal statistical inference of confidence limits.

Phylogenetic Classification

A Linnean classification based on the inferred phylogenetic tree was prepared using the methods described by Wiley (1981). These conventions include optimal preservation of hierarchical information provided by the phylogenetic tree in the classification, and the indication of poorly resolved sections of the tree through standardized annotation of the classification at the appropriate taxonomic ranks (e.g., use of *sedis mutabilis* to indicate a series of taxa included in a polytomy).

Comparative Analyses

A number of attributes of considerable ecological importance that are not amenable to discrete coding and determination of homology were compiled and mapped *a posteriori* onto the phylogenetic tree(s) hypothesized using the characters defined above (using the same character optimization used in the actual tree). Such mappings permit comparative study of convergence and adaptation within a historical context (Brooks and McLennan, 1991; Harvey and Pagel, 1991), and were employed in ongoing analyses of other anseriform tribes (Livezey, in press *a*, in press *b*). These attributes include body mass (unweighted mean of sexes), mean clutch size, mean egg mass, relative clutch mass (mean mass of clutch divided by mean female body mass), preferred nest site (terrestrial or cavity), perching habit, relative frequency of diving, and period of activity (diurnal, crepuscular, or nocturnal), as well as geographic distribution; data for these characters were taken from specimen labels, unpublished data, and the literature (Phillips, 1922; Delacour, 1954; Johnsgard, 1960*a*, 1960*b*, 1961*a*, 1962, 1963, 1965, 1967, 1978; Schönwetter, 1961; Weller, 1964*a*, 1964*b*, 1964*c*, 1964*d*; Frith, 1967; Madge and Burn, 1988; Rohwer, 1988; Marchant and Higgins, 1990; McNeil et al., 1992). Distributions of these attributes on the phylogenetic tree(s) were examined and illustrated using the software MacClade 3.01 (Maddison and Maddison, 1992). Both PAUP and MacClade were implemented on a Macintosh Quadra 800.

RESULTS

Shortest Trees

Three trees of minimal length 91 were found using the data described in Appendix 1 and given in Appendix 2. Each tree was completely dichotomous, and had a consistency index of 0.879 (0.766 excluding autapomorphies), a homoplasy index of 0.121, a retention index of 0.750, and a rescaled consistency index of 0.659 (Fig. 1). Monophyly of the Dendrocygninae (i.e., a sister-group relationship between *Thalassornis* and *Dendrocygna*) is supported by three characters.

One of the characters supportive of subfamilial monophyly—a feature of the natal plumage pattern (characters 19)—proved to be difficult to code for *Thalassornis* (Fig. 2; Appendices 1, 2). An alternative interpretation of this character and a related character of the unique natal facial pattern for *Thalassornis* (character 23) was apparent and also was analyzed for possible topological effect. In this alternative coding scheme, character 19 is simplified to a binary character (merging states "b" and "c" into a single derived state) in which *Thalassornis* retains the primitive state, thereby deleting one synapomorphy for the subfamily. This change, however, leads to an alternative interpretation for character 23 in which *Thalassornis* is judged to possess the derived state (obscured by the absence of a pale, dorsal boundary), adding a new synapomorphy for the subfamily. Taken together, these two alternative codings are mutually compensatory in their support for the monophyly of *Thalassornis* and *Dendrocygna,* have no topological impact on the analysis, and are not considered further.

Monophyly of *Dendrocygna* is supported by eight unambiguous character changes (Fig. 1, 2). The three most-parsimonious trees confirm two moderately well-supported clades (Fig. 1): (1) *D. autumnalis* + *D. viduata,* and (2) the other six species of *Dendrocygna*. Within the latter, the three shortest trees defined two groups: (1) *D. guttata* + *D. arborea* (supported by three synapomorphies), and (2) an unresolved trichotomy (supported by one unambiguous synapomorphy) involving *D. eytoni, D. bicolor,* and the clade *D. arcuata* + *D. javanica* (the last two united by three synapomorphies).

Monophyly of each of the species in the ingroup was confirmed by a number of autapomorphies, reflecting a diversity of unique, species-specific characters (at least in the context of this subfamily). *Thalassornis* was the most divergent, having
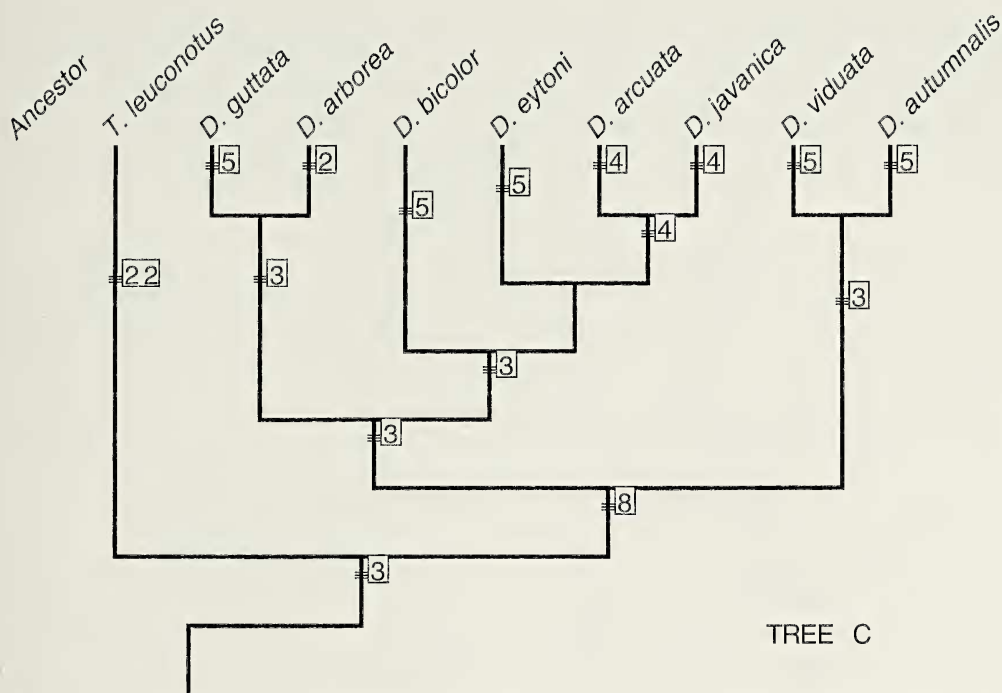
TREE   A

TREE   B
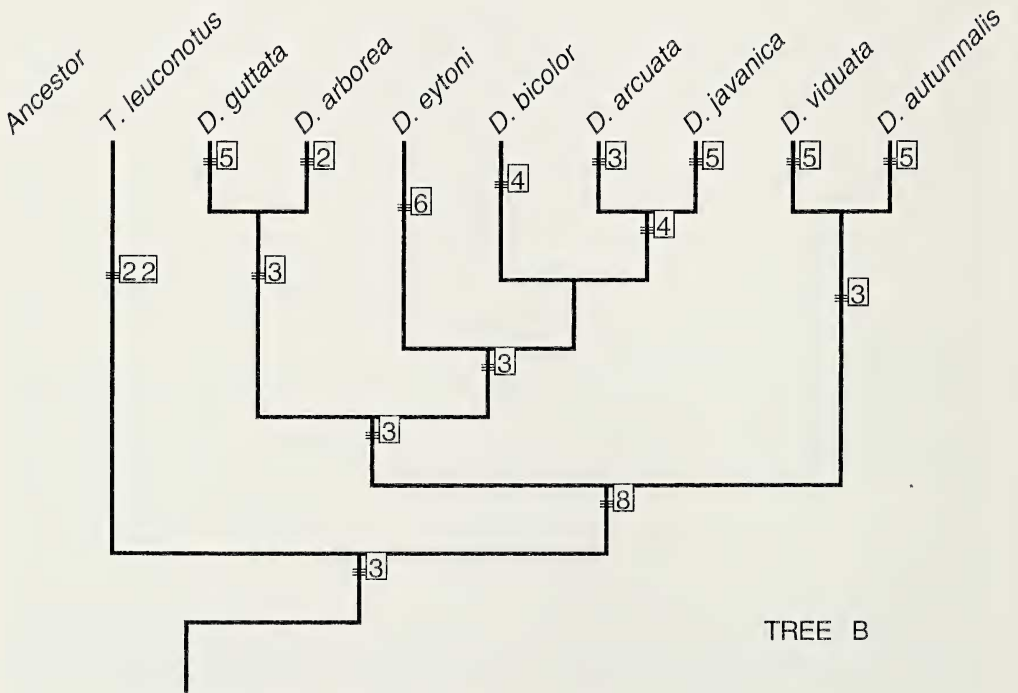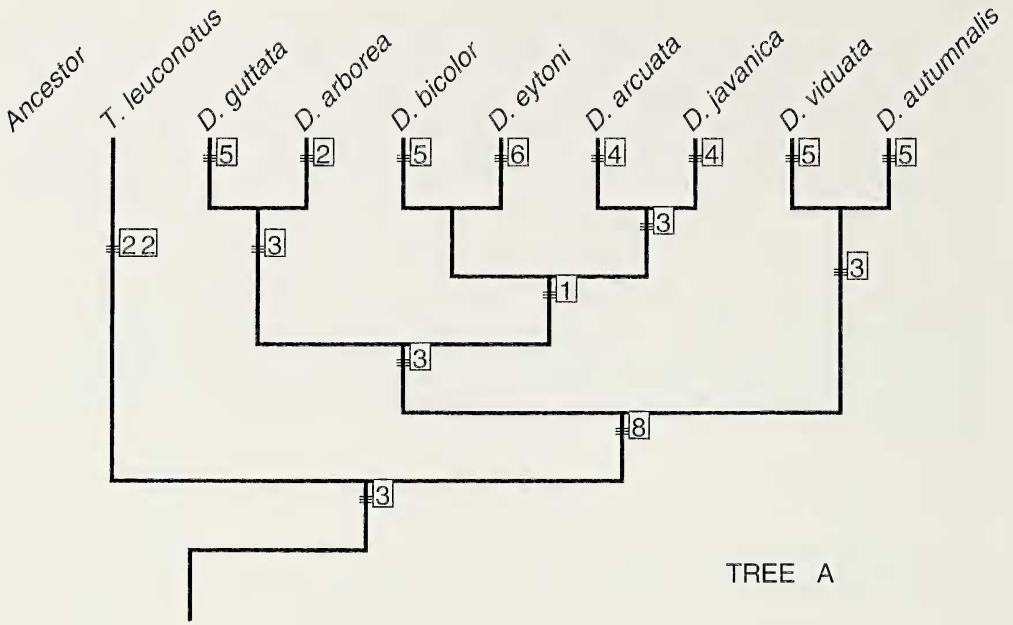
Fig. 1. (Left, and above)—Three shortest phylogenetic trees (A–C) for *Dendrocygna* and *Thalassornis* based on a branch-and-bound analysis of 68 morphological characters. Numbers of unambiguous character changes supporting each branch are shown in adjacent boxes.

22 unambiguous autapomorphies of which 12 were skeletal characters. Each species of *Dendrocygna* had between two and six unambiguous autapomorphies in the present data set, with the most divergent species being *D. eytoni* (Fig. 1). Identities of unambiguous characters supportive of branches in the three shortest trees are shown in Fig. 2.

Topological Robustness

A consensus tree of 1000 bootstrapped replications (Fig. 3) confirmed the monophyly of *Dendrocygna* and all elements common to the three most-parsimonious trees (Fig. 1, 2). Percentages of replicates in which each branch was conserved varied from 65% (for *Dendrocygna* exclusive of *viduata* and *autumnalis*) to 100% (for the genus *Dendrocygna*).

Consistencies of Characters

Fifty-nine of the 68 characters used in the phylogenetic analyses had unit consistency in the inferred shortest tree; i.e., each character was hypothesized to have changed only once per derived state defined (Appendix 1). Eight binary (two-state) characters had consistency indices of 0.50, i.e., each was hypothesized to have undergone one instance of reversal or convergence in the inferred tree: two natal (characters 18 and 20) and seven definitive (characters 28, 41, 53, 54, 57, and 67). One three-state character of the definitive integument (characters 24 and
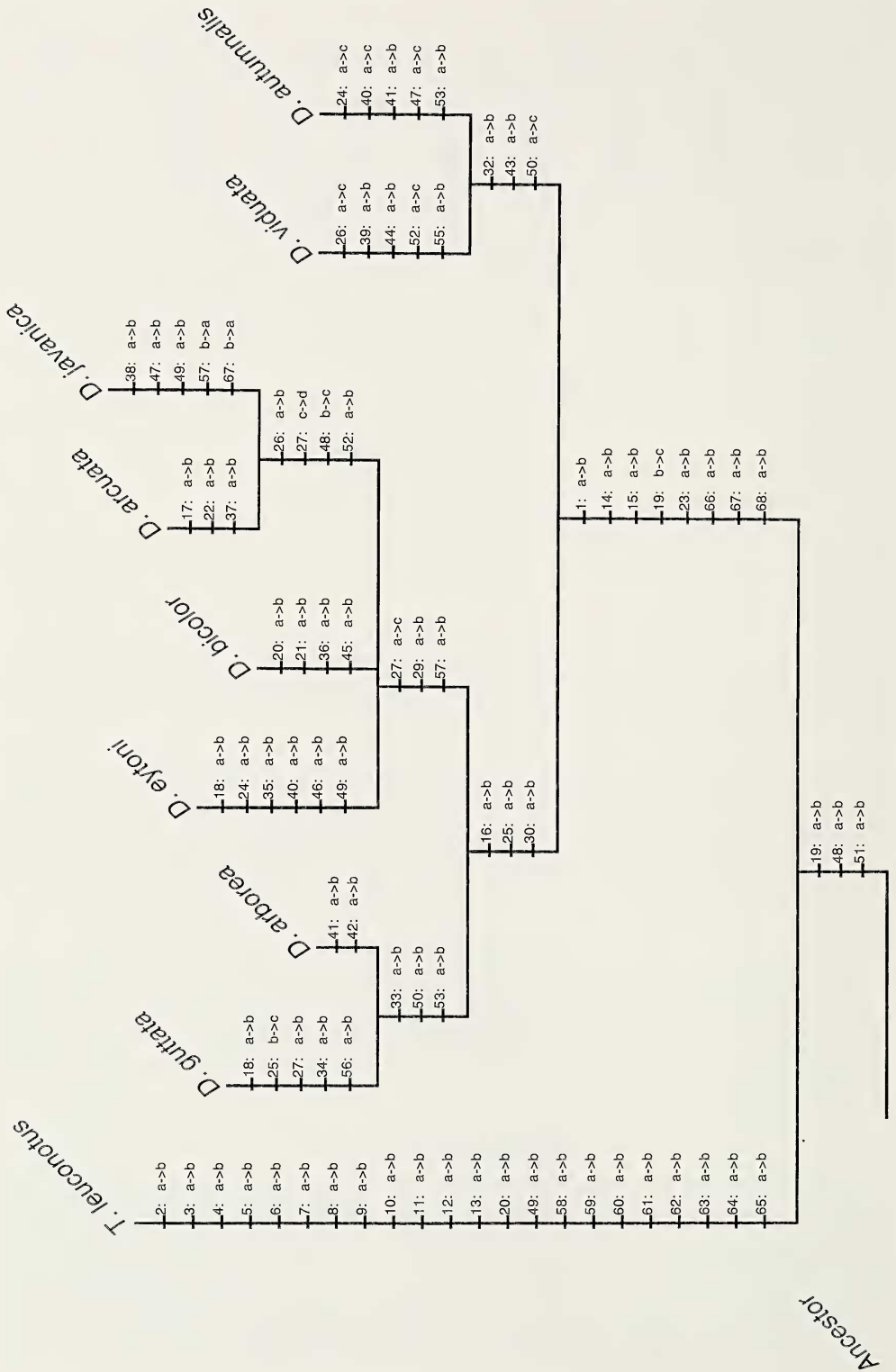
52) had consistency indices of 0.667, i.e., one instance of reversal or convergence involving one of the two derived states was hypothesized. Only one character (caudal darkness of nuchal stripe of adults, character 49) was hypothesized to have undergone two instances of convergence (i.e., three separate changes from a primitive to a derived state), and each was inferred to have been an autapomorphic loss (in *Thalassornis, Dendrocygna eytoni,* and *D. javanica*).

Phylogenetic Classification

A classification of the species of *Dendrocygna* and *Thalassornis,* which reflects the phylogenetic inferences made here (Fig. 1–3), is presented in Appendix 3. The sister relationship between *Dendrocygna* and *Thalassornis* is supported by only three characters, one of which is interpretable in at least two ways. Under the hypothesis of a monophyletic, bigeneric Dendrocygninae, the genera are distinguished (redundantly) at tribal level; recognition of tribes is consistent with the classificatory ranks employed in other subfamilies of Anatidae (Livezey, 1986, 1989) and permits the inclusion of several fossil species related to *Dendrocygna* (e.g., *Dendrochen, Mionetta*) within the Dendrocygnini should further analysis provide needed resolution (Livezey and Martin, 1988). Within the genus *Dendrocygna,* the primary bifurcation is represented at the subgeneric level; in the larger of the two subgenera, two multispecific groups are indicated. Because of the included unresolved trichotomy and only modest robustness of included clades, the four species included in Infragenus *Dendrocygna* are considered to be of uncertain sequence (*sedis mutabilis*).

Mapping of Attributes on Trees

Eight ecomorphological attributes showing variation within the ingroup were mapped onto the first of the three shortest phylogenetic trees (Fig. 1), noting any differences in interpretation indicated by the other two equally parsimonious trees (Fig. 1). Comparison with outgroups (*Anseranas,* Anserinae) indicates that the entire clade (*Thalassornis* and *Dendrocygna*) has undergone a substantial decrease in body mass, followed by one further autapomorphic decrease in size in *Dendrocygna javanica* and two autapomorphic (partial) reversals in size (i.e., derived increases) in *D. arborea* and *D. autumnalis* (Fig. 4). Clutch size appears to have undergone an increase in the ancestor of the subfamily, with three further autapomorphic increases hypothesized in *Dendrocygna guttata, D. eytoni,* and *D. autumnalis* (Fig. 4). Egg mass shows an opposite trend, evidently having undergone an initial decrease in the common ancestor of the subfamily, followed by a further decrease in *Dendrocygna,* with three additional, independent decreases in *D. viduata, D. eytoni,* and the sister-species *D. arcuata* and *D. javanica* (Fig. 4). One of the other two equally parsimonious trees, in which *D. bicolor* is placed as the sister species to the other three members of that clade (Fig. 1), requires only two changes in egg mass within *Dendrocygna.* Relative clutch mass, which represents clutch size and egg mass relative to female body mass, shows a complicated

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Fig. 2.—Tree detailing unambiguous character changes supporting branches of shortest phylogenetic trees for *Dendrocygna* and *Thalassornis* based on a branch-and-bound analysis of 68 morphological characters (Fig. 1). Characters (numbered) and associated state changes (letters) are shown beside respective branches (see Appendix 1 for explanation).
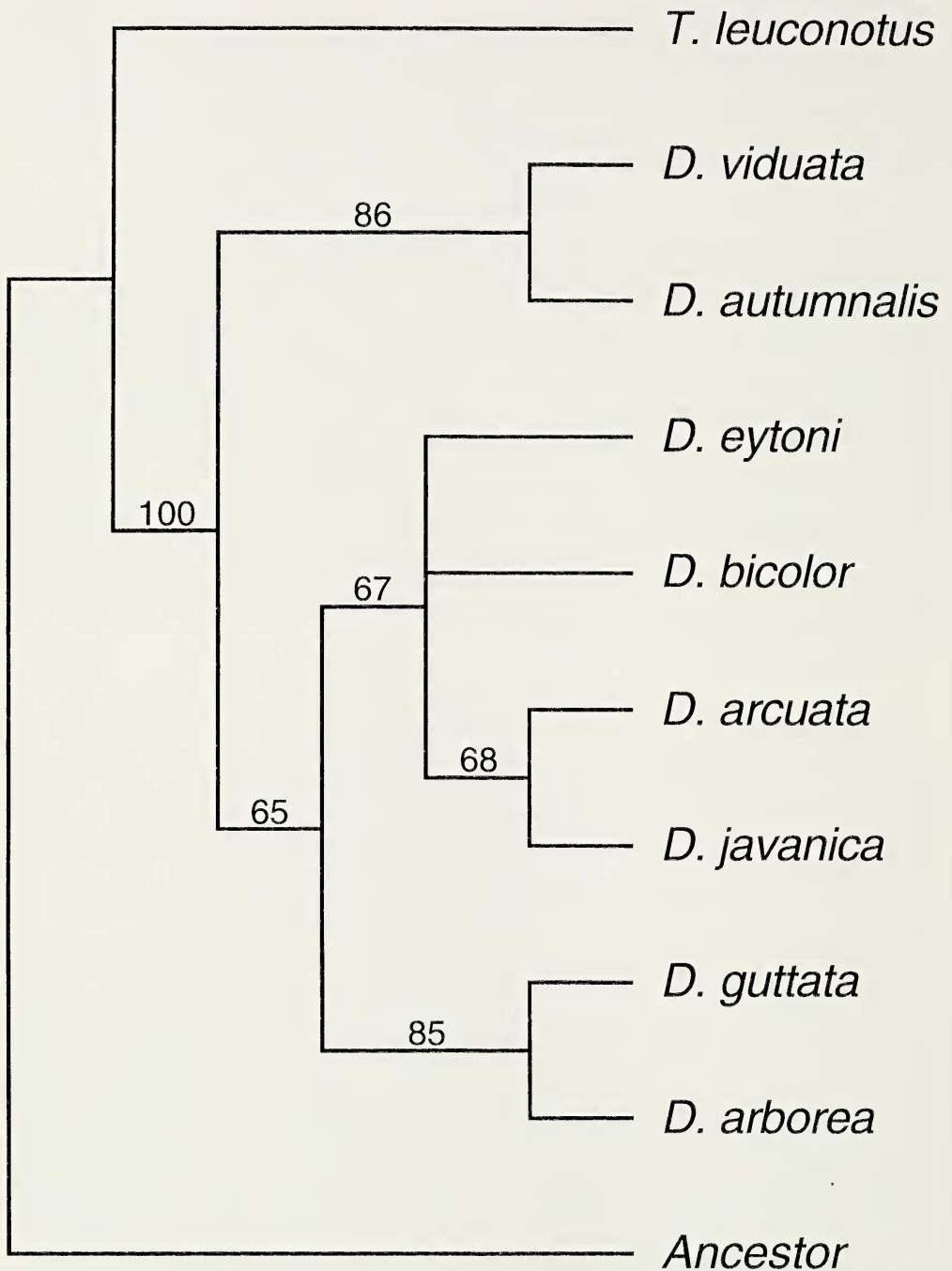
Fig. 3.—Majority-rule consensus tree of 1000 bootstrapped replications (using branch-and-bound) of solution set (Fig. 1). Percentages of replications in which each branch was conserved are indicated.
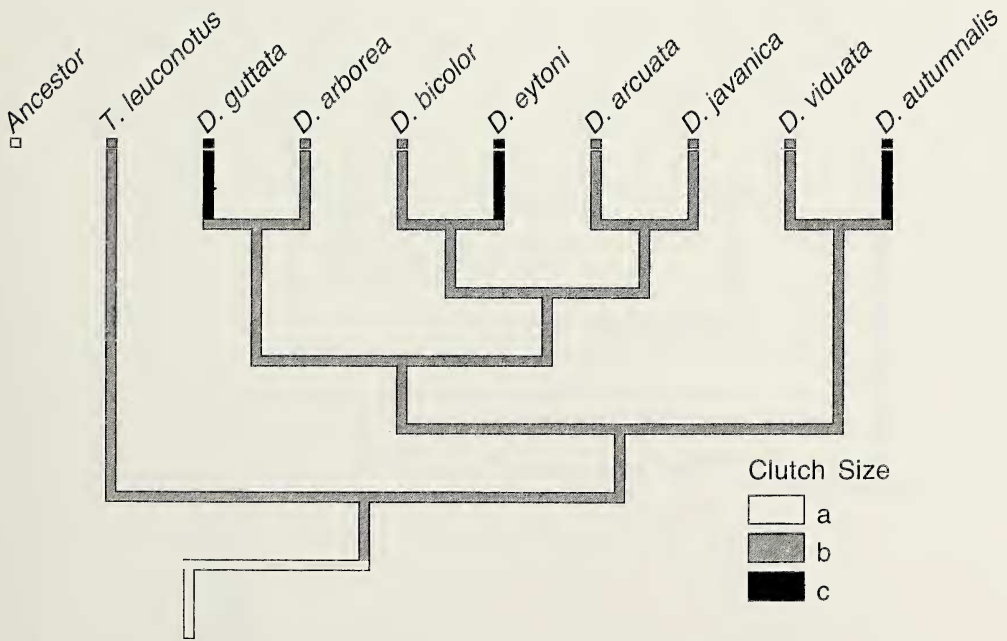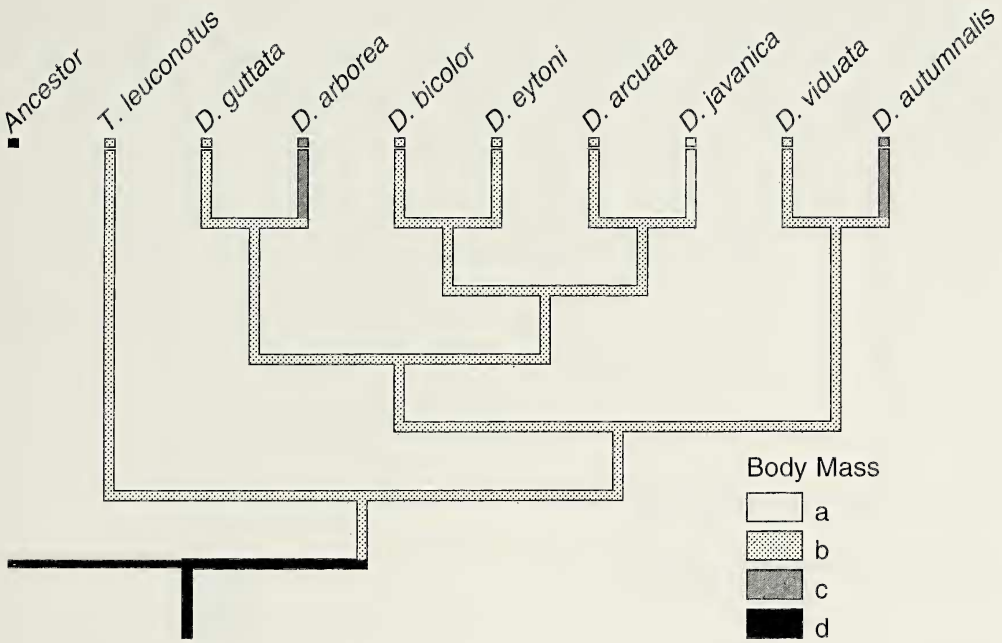
Fig. 4.—Evolutionary trends in selected ecomorphological characters of the Dendrocygninae (characters and states defined in Appendix 1, tabulated in Appendix 2): body mass; clutch size; egg mass; relative clutch mass; preferred nest site; perching habit; diving habit; and primary period of activity.
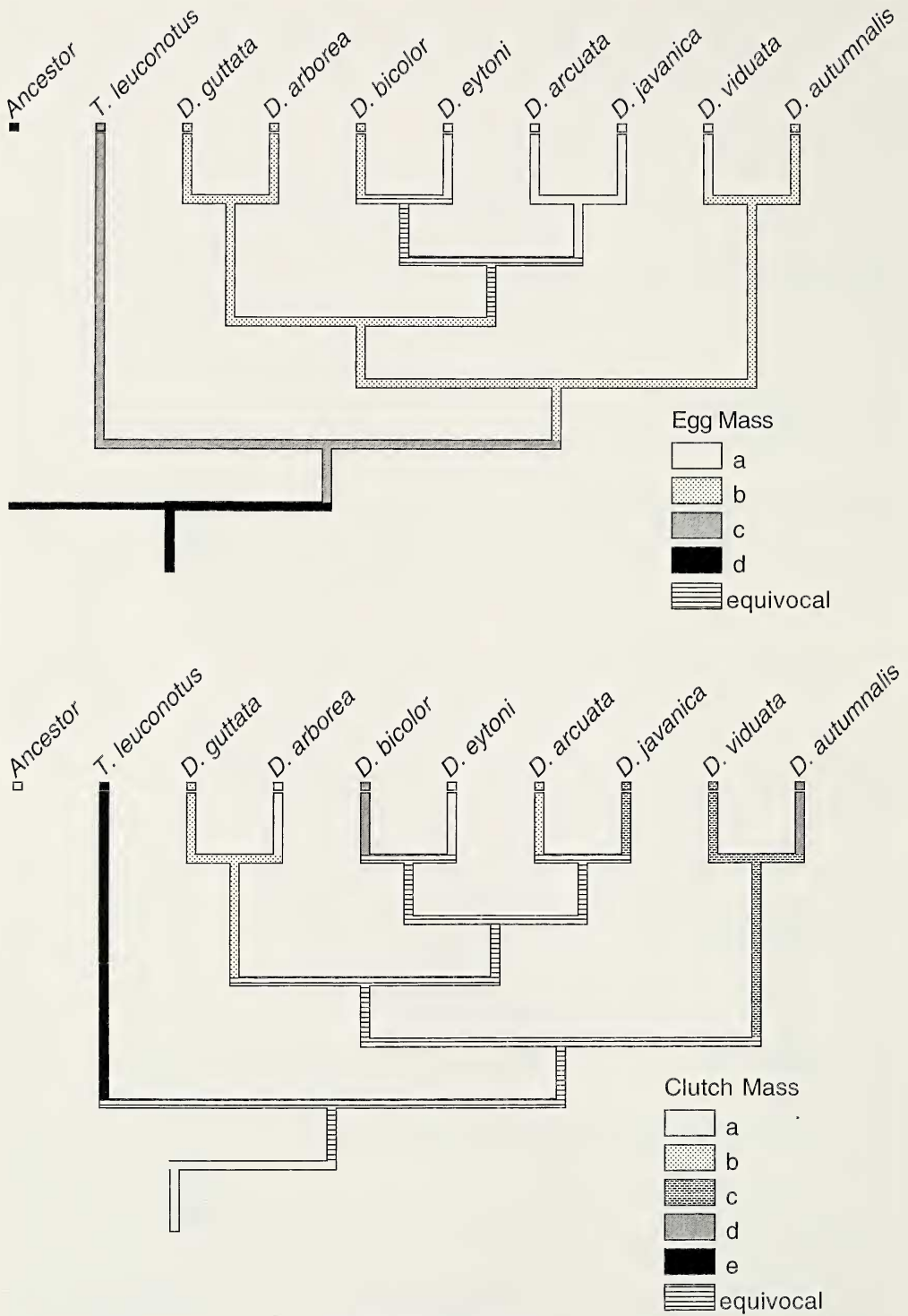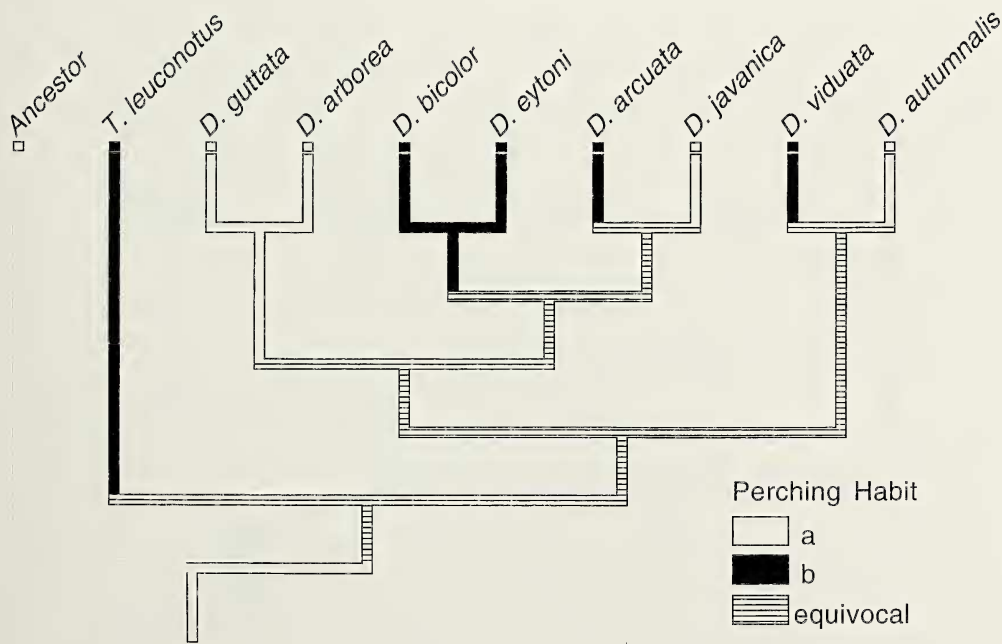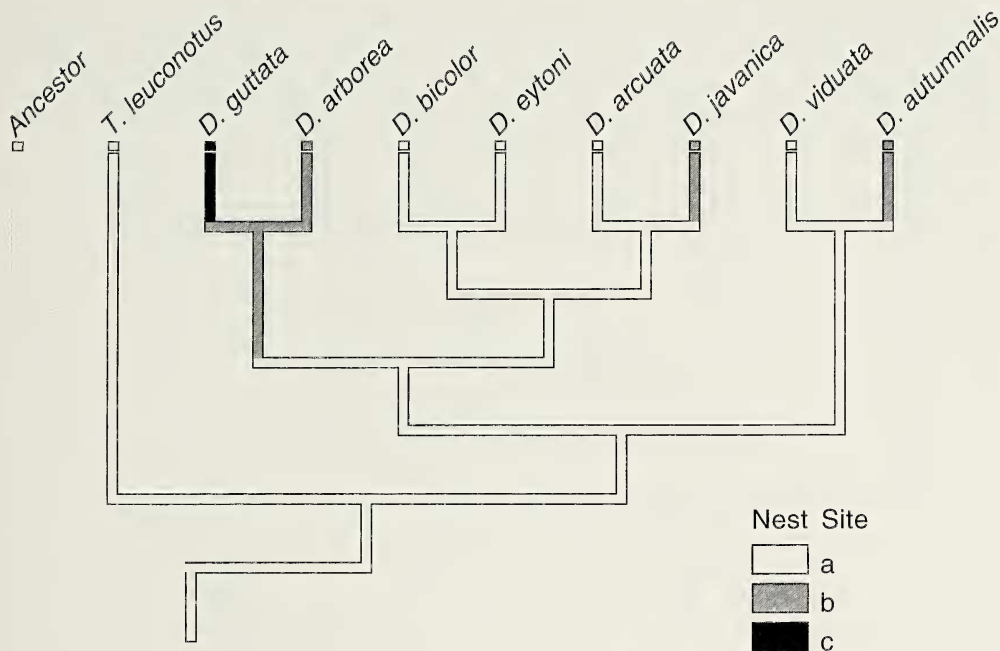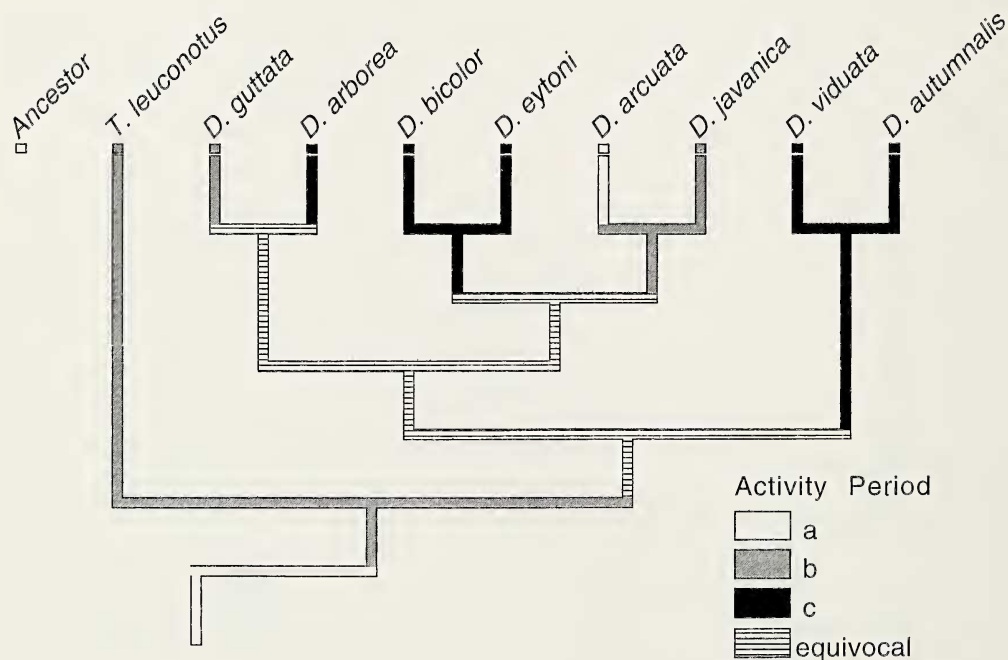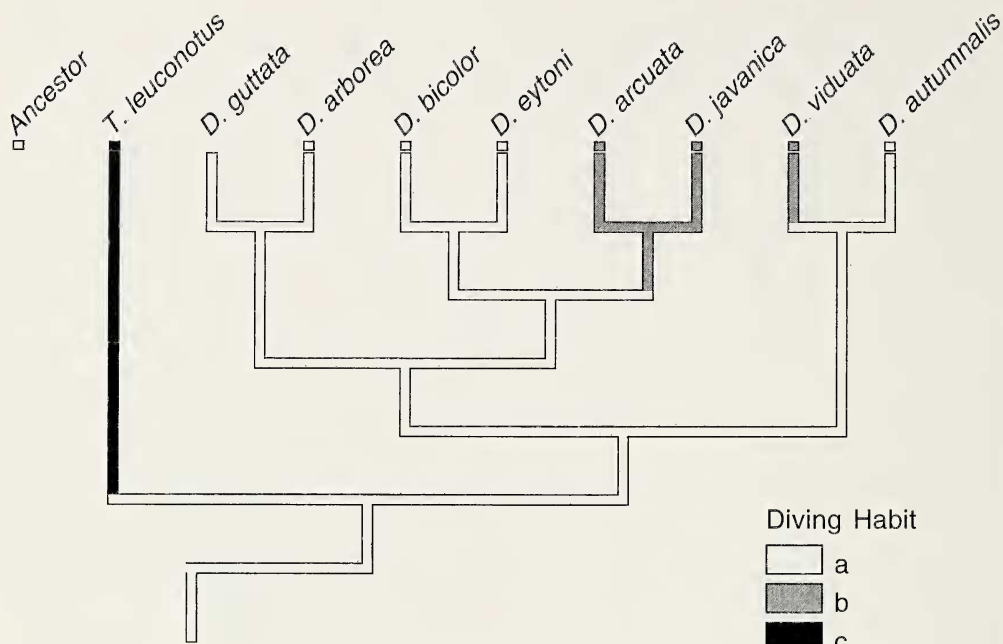
Fig. 4.—Continued.

Fig. 4.—Continued.

Fig. 4.—Continued.

evolutionary pattern in the subfamily, and the states of the majority of the ancestral stems of the ingroup remain in doubt. Available data indicate, however, that relative clutch mass: (1) underwent a substantial increase in *Thalassornis,* (2) underwent modest independent decreases in *Dendrocygna arborea* and *D. eytoni,* and (3) underwent modest autapomorphic increases in *D. bicolor* and *D. autumnalis* (Fig. 4).

The primitive preference for nest sites was inferred to be terrestrial, and the present phylogenetic tree and available data on preferences indicates that shifts to cavity nesting occurred independently in *Dendrocygna autumnalis* and *D. javanica,* and synapomorphically in the sister-species *D. arborea* and (especially) *D. guttata* (Fig. 4). Perching habit, evidently only weakly associated with nesting preferences (Livezey, 1986, 1991), was hypothesized to be the primitive state for the Dendrocygninae, with apparent reversals (secondary losses) independently in *D. viduata, D. arcuata,* and the sister-species *D. eytoni* and *D. bicolor* (Fig. 4).

Diving habit showed a distinct evolutionary pattern in the Dendrocygninae; the primitive lack of diving behavior evidently underwent a profound, derived specialization in *Thalassornis,* with less marked, independent shifts to moderate use of diving in *D. viduata* and (synapomorphically) in the sister-species *D. arcuata* and *D. javanica* (Fig. 4). Variation in diel activity pattern revealed less clear evolutionary trends, and the states hypothesized for basal stems remain indeterminate. However, the present analysis indicates: (1) that the primitive state of diurnal activity changed to crepuscular activity in the ancestor of the Dendrocygninae; (2) possibly independent, subsequent shifts to nocturnality in *D. viduata* + *D. autumnalis, D. eytoni* + *D. bicolor,* and *D. arborea*; and (3) a reversal to diurnality in *D. arcuata* (Fig. 4).

DISCUSSION

Phylogenetic Hypothesis and Previous Classifications

Summary of Inferences. —The present analysis provides only moderate support for the monophyly of the genera *Thalassornis* and *Dendrocygna* (three synapomorphies uniting the two genera exclusive of all outgroups compared), but documents substantial evidence for monophyly of the diverse species of *Dendrocygna* (Fig. 1–3). Evidence is presented in support of a basal bifurcation in *Dendrocygna,* in which two species (*D. viduata* and *D. autumnalis*) are considered to be the sister-group to other *Dendrocygna* (also monophyletic). Within the latter clade, three branches were supported and one unresolved trichotomy was found (Fig. 1–3); the two species-pairs were *D. arcuata* + *D. javanica* and *D. guttata* + *D. arborea.* All species of *Dendrocygna* and (especially) *Thalassornis* show considerable autapomorphic divergence (Fig. 1, 2).

Early Taxonomic Arrangements within Dendrocygna. —Much of the early taxonomic literature that treated *Dendrocygna* concerned the diagnosis of species and delimitation of geographic distributions, and several new generic taxa were erected without the benefit of broad comparative work (e.g., Eyton, 1838; Sclater, 1864; Salvadori, 1895). A few general classifications and monographs, however, attempted systematic arrangements of species within the genus, although in large part the intuitions of these workers are reflected only by the sequence of species they adopted and the basis for these decisions remains obscure. For example, Salvadori (1895) listed, without justification, the species of *Dendrocygna* in the following order: *viduata, bicolor* (as *fulva*)*, arcuata, javanica, autumnalis* (followed by *discolor,* here provisionally merged)*, arborea, guttata,* and *eytoni.* Phillips

(1922) followed this sequence exactly. Peters (1931) also adopted this sequence, with the exception that *discolor* was treated as a subspecies of *D. autumnalis,* a practice followed in subsequent classifications (e.g., Boetticher, 1942, 1952; Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1961*a*, 1965, 1978, 1979; Wolters, 1976; Sibley and Monroe, 1990; Hoyo et al., 1992).

Classifications by Delacour and Johnsgard. — In their classic systematic revision of the Anatidae, Delacour and Mayr (1945:11) divided *Dendrocygna* into three groups: (1) a "primitive" group consisting of *D. arborea* and *D. guttata*; (2) the "somewhat isolated" species *D. autumnalis*; and (3) the remaining five "closely related" species in the genus, within which *D. bicolor* and *D. arcuata* were termed a "superspecies" and *D. viduata* was described as "specialized." Accordingly, these authors (1945:37) proposed the following taxonomic sequence for the species of *Dendrocygna: arborea, guttata, autumnalis, javanica, bicolor + arcuata* (bracketed together), *eytoni,* and *viduata.* Delacour (1954:27–30), however, admitted to considerable indecision as to the appropriate classification of species within *Dendrocygna,* and presented apparently contradictory evidence and groupings of the constituent species. Delacour (1954:29–30) decided to adopt the following sequence for *Dendrocygna,* explicitly citing only similarities of the natal plumage as justification: *guttata* and *eytoni* at the beginning and considered primitive; followed by *arcuata, bicolor,* and *arborea*; and ending with the "more isolated" species *javanica, viduata,* and *autumnalis.*

Johnsgard (1961*a*) also presented the conflicting evidence for groupings within *Dendrocygna,* primarily emphasizing behavioral similarities (especially courtship displays), natal patterns, and geographical distributions. Johnsgard (1961*a*:fig. 1) summarized his assessment of this information in an intuitive evolutionary tree that depicted the following subgeneric groups of *Dendrocygna:* (1) *guttata* and *eytoni*; (2) *arborea* and *autumnalis,* together joined with *viduata*; and (3) *bicolor* and *arcuata,* in turn united with *javanica.* However, Johnsgard (1965) later presented the following sequence for *Dendrocygna,* which contradicts the groupings he had defined previously: *guttata, eytoni, bicolor + arcuata* (united as a superspecies), *javanica, viduata, arborea,* and *autumnalis.* This sequence was followed in later works by Johnsgard (1978, 1979) as well as in recent monographs (Sibley and Monroe, 1990; Hoyo et al., 1992).

The empirical basis for the groupings and sequence proposed by Johnsgard (1961*a*, 1965, 1978, 1979) consists of a narrative of similarities and differences of plumage and behavior (many not comparably discussed or described for all species), as well as consideration of geographical proximities of species, and as such does not lend itself to quantitative analysis or incorporation into phylogenetic analyses. However, one comparison of the tree presented by Johnsgard (1961*a*: fig. 1) can be made through the calculation of the total length of his tree using the characters analyzed in the present study (Appendices 1, 2) with that for the shortest tree for the same data (Fig. 1). Using the software MacClade 3.0 (Maddison and Maddison, 1992), the tree proposed by Johnsgard (1961*a*) requires an additional 12 character changes relative to the shortest tree for the same data matrix, a 13% increase in length.

Ancient Divergences and Phylogenetic Reconstruction

Autapomorphies, Distinctness, and Perceptions of Relationships. — In light of the relative abundance of plumage characters in the nine species of the ingroup, the incomplete resolution and only modest support for several of the included clades

is disappointing (Fig. 1–3). However, all lineages within the Dendrocygninae show considerable autapomorphic (generally unique) character evolution; this is particularly true of *Thalassornis* (Fig. 1, 2). The combination of the heterogeneous distribution of synapomorphies and the prevalence of autapomorphy results in a clade of uniquely divergent species without clear evidence of natural subgroups, corroborating the suggestion by Delacour (1954:30) that: "The present species of Whistling Ducks have, no doubt, been fixed for a very long time and their common ancestor is far away in the past."

A strong tradition of "intuitive phenetics" has dominated the systematics of waterfowl until recent years, in which simple assessments of similarity using changing and inconsistently applied suites of characters constitute the foundation of most classifications (e.g., Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1961*a*, 1965, 1978). Most such assessments involve vague and nonstandardized terminology that is not conducive to the elucidation of any specific phylogenetic hypothesis. For example, Johnsgard (1978:10) wrote: "This species [*D. eytoni*] appears to be generally intermediate in its evolutionary affinities between the extreme represented by the spotted whistling duck [*D. guttata*] and the central group represented by the wandering [*D. arcuata*], fulvous [*D. bicolor*], and lesser whistling ducks [*D. javanica*] . . . , with somewhat closer affinities to the latter than to the former." Also, Johnsgard (1978:12) suggested that *D. bicolor* ". . . might well be regarded as the core of the genus *Dendrocygna,* with its nearest relatives being the wandering [*D. arcuata*] and lesser whistling ducks [*D. javanica*]." A common confusion between distinctness and phylogenetic relationship is illustrated by the discussion of *D. viduata* by Johnsgard (1978:19): ". . . [it] appears to be relatively isolated from the other species of *Dendrocygna.* Probably its nearest, if not extremely close, relative is the black-bellied whistling duck [*D. autumnalis*]." Capricious favoring of one suite of characters (often inadequately described) over another source of evidence is exemplified by the following discussion by Johnsgard (1961*a*:73): "Adult plumage patterns are of little value in showing relationships in this genus [*Dendrocygna*], and it is of interest that two species (*D. guttata* and *D. arborea*) which have outwardly similar adult plumages are probably not at all closely related. Both are island species (*arborea* West Indies, *guttata* East Indies) which are allopatric with nearly all other whistling ducks, and I believe that this dull, spotted adult plumage is a secondary, convergent, [*sic*] derivation."

This obfuscation of phylogenetic relationships within *Dendrocygna* has been worsened by two traditional methods of taxonomic inference. The first is the grouping of species by symplesiomorphy, in which the presence of a primitive character (i.e., the absence of a derived character) is used as a grouping criterion, leading to the recognition of paraphyletic or polyphyletic taxa (Wiley, 1981). The shared retention of plesiomorphies was the primary justification for the inclusion of *Dendrocygna* with the geese and swans in the same subfamily by Delacour and Mayr (1945), Delacour (1954), and Johnsgard (1965, 1978). An example of a symplesiomorphically defined group within *Dendrocygna* is the placing of *D. guttata* with *D. eytoni* by Delacour (1954) and followed, at least by adjacent placements in sequence of species, by Johnsgard (1961*a*, 1965, 1978, 1979). The second major misleading practice has been the idea that simple distinctness or phenetic differences (typically the accumulation of autapomorphies) indicates distant relationship to other species under study. An example of this kind of inference in *Dendrocygna* is the adjacent, terminal sequencing by Delacour (1954:29–30)

of three species considered to be "more isolated"—*D. javanica, D. viduata,* and *D. autumnalis*—an instance exacerbated by the additional implication (perhaps unintended) that mutually unique divergences somehow phylogenetically unite these species.

Fossil Radiations and "Missing" Lineages.—Weak support for the monophyly of the Dendrocygninae and poor resolution of phylogenetic relationships within *Dendrocygna* may reflect, in part, the absence by extinction of analytically important, transitional lineages in the group. The likelihood that modern members of the Dendrocygninae represent but a small vestige of a past radiation of species is suggested also by the geographical distribution and diversity of fossil ducks of comparable grade (Wetmore, 1924; Miller, 1944; Brodkorb, 1964; Howard, 1964; Livezey and Martin, 1988). Unfortunately, inclusion of these forms in the present analysis is not feasible given the heavy use of characters of the integument, characters which are not available for study in fossil species.

Reproductive Isolation.—Although interspecific hybridization is known among species of *Dendrocygna,* there are no confirmed records of hybridization between members of the genus and those of any other in the Anatidae (Johnsgard, 1960*b,* 1963; Scherer and Hilsberg, 1982). Moreover, most interspecific hybrids within *Dendrocygna* involved captive birds and undetermined fertility of offspring (Johnsgard, 1960*b*). Traditionally, the absence of interfertility has been interpreted as the adaptive product of selection against interspecific hybridization and as evidence of distant phylogenetic relationship (Sibley, 1957; Johnsgard, 1960*b,* 1963; Scherer and Hilsberg, 1982). Even if the phylogenetic interpretation is assumed to be valid, inferences concerning phylogenetic relationships are not possible in a group like the Dendrocygninae, in which interspecific hybridization is rare or nonexistent for most or all members. Alternatively, reproductive isolation can be interpreted as the accumulation of genetic, karyotypic, behavioral, or morphological factors that deter mating and successful reproduction (Livezey, 1991). Viewed in this way, such incompatibilities would be expected to arise in comparatively ancient, conspicuously autapomorphic lineages such as those that compose the Dendrocygninae; whether such "barriers" were the subject of natural selection against hybridization cannot be assessed, at least not in this taxonomic group.

Evolutionary Patterns

Sexual Dimorphism.—Like the screamers (Anhimidae), Magpie Goose (Anseranatidae), geese and swans (Anserinae), and the Freckled Duck (Stictonettinae), the Dendrocygninae retain the plesiomorphy of sexual monochromatism with a single molt and plumage per annual cycle (Delacour, 1954, 1959; Johnsgard, 1962; Kear, 1970). In addition, the Dendrocygninae lack any significant sexual size dimorphism; examination of mean body masses (Livezey and Humphrey, 1984) in the context of the generic phylogenetic tree presented by Livezey (1986) indicates that this character also is probably primitive for the Anatidae. This retention of plesiomorphies obviates any discussion of the possible selective advantages of sexual dimorphism in the Dendrocygninae (Sibley, 1957; Sigurjónsdóttir, 1981; Scott and Clutton-Brock, 1989).

Social Behavior.—Species of *Dendrocygna* are nearly identical in precopulatory and postcopulatory displays and share a number of behavioral characteristics (Johnsgard, 1961*a,* 1962): precopulatory "head-dipping," mutual postcopulatory displays, the absence of a true "triumph ceremony," highly developed aggressive

behavior, "head-back" and "head-low-and-forward" threat postures, and flight-intention movements consisting of lateral head-shaking. *Thalassornis* shares a number of these behavioral characters with *Dendrocygna* (Johnsgard, 1967, 1978), but the absence of polarities for these behavioral characters renders a phylogenetic interpretation problematic. Detailed ethological data are not available for several species of *Dendrocygna,* precluding a phylogenetic assessment of potentially informative interspecific differences in voice and relative frequencies of threat displays noted by Johnsgard (1961*a*). Given that *Anseranas* and the Anserinae reach sexual maturity at 2–3 years of age (Kear, 1970), it seems likely that the attainment of sexual maturity at one year of age in the Dendrocygninae is a derived condition, one possibly related in part to reduced body size.

Parameters of Reproduction. — The pervasive primitiveness of the Dendrocygninae also characterizes a number of reproductive parameters, including monogamy, protracted pair-bonds, and participation by males in nest construction and brood-rearing and (at least in some species) incubation (Delacour and Mayr, 1945; Delacour, 1954, 1959; Johnsgard, 1961*a*, 1962, 1965, 1978; Weller, 1964*b*; Kear, 1970; Murton and Kear, 1975; Scott and Clutton-Brock, 1989). Like most Anatidae, most or all members of the Dendrocygninae participate in intraspecific and interspecific nest parasitism, another evidently primitive habit (Eadie et al., 1988; Rohwer and Freeman, 1989). However, formation of brood amalgamations or crèches, a behavior of undetermined polarity in the Anatidae, has not been reported for *Dendrocygna* or *Thalassornis* (Eadie et al., 1988).

The entire Dendrocygninae are united by several pronounced, evidently derived ecomorphological attributes, including a decrease in body mass, an increase in clutch size, and a decrease in egg mass (Fig. 4). Considered together, however, a distinctly different evolutionary pattern in relative investment in reproduction in the Dendrocygninae emerges, in which a variable and modest increase characterizes the subfamily generally, and *Thalassornis* attains a marked, autapomorphic extreme (Fig. 4). Preferred nest sites and perching habit show less clear evolutionary patterns (Fig. 4); in both attributes, however, the present phylogenetic hypothesis indicates that cavity-nesting and terrestrial roosting are the apomorphic states in the Dendrocygninae, and that both have been derived independently more than once within *Dendrocygna.*

Foraging and Activity Patterns. — Both *Dendrocygna* and *Thalassornis* are primarily vegetarian in feeding habit, a presumably primitive condition shared with the Anhimidae, *Anseranas,* the Anserinae, and most other Anatidae (Delacour, 1954, 1959; Johnsgard, 1978; McNeil et al., 1992). Species of *Dendrocygna* generally employ surface feeding and upending to reach their food, although members of all species occasionally dive (Weller, 1964*a*; Johnsgard, 1978; McNeil et al., 1992). Comparatively heavy reliance on diving during foraging, evidently a repeatedly derived condition in the Anatidae (Johnsgard, 1962; Livezey, 1986), is hypothesized here to have evolved three times independently in the Dendrocygninae (Fig. 4). Frequency of diving may be associated with interspecific differences in relative foot size within *Dendrocygna* (Rylander and Bolen, 1970; Bolen and Rylander, 1974, 1983; Siegfried, 1973). Moreover, reliance on diving, with concomitant morphological specialization for underwater propulsion (Woolfenden, 1961; Raikow, 1971; Livezey, 1986), underlies many of the autapomorphies in *Thalassornis* (Fig. 1). Many of the diving-related skeletal apomorphies in *Thalassornis* are convergent with those of diving ducks in other tribes of the Anatidae, especially the Oxyurini (Livezey, 1986; Faith, 1989). A derived trend toward

crepuscular and nocturnal activity also characterizes the Dendrocygninae (Fig. 4), with a majority of the species of *Dendrocygna* best described as nocturnal (Delacour, 1954, 1959; Johnsgard, 1978; McNeil et al., 1992). Possible selective advantages of nocturnal foraging in the vegetarian, largely tropical Dendrocygninae are not obvious, but avoidance of high temperatures and diurnal predators are among the most plausible candidates (McNeil et al., 1992). Any proximate explanation of nocturnality in Dendrocygninae should take into account the reversal to predominantly diurnal activity shown by *D. arcuata* (Fig. 4).

Biogeography

Distributional Patterns. — The phylogenetic relationships for the Dendrocygninae (Fig. 1) indicates a biogeographical pattern not explainable by a simple hypothesis of historical vicariance (Delacour, 1954, 1959; Weller, 1964*d*; Bolen and Rylander, 1983). The subfamily is almost completely limited to a circumglobal, equatorial band, and member species are strictly tropical and subtropical in habitat. Seven of nine species are limited in distribution to single, variably overlapping geographical regions within this equatorial belt. *Dendrocygna bicolor* and *D. viduata,* however, are distributed in two or more disjunct continental areas and are extensively sympatric in South America and Africa; the transatlantic distribution of *D. viduata* prompted Sclater (1864) to speculate erroneously that the species had been introduced into the Neotropics from Africa by slavers. Within the subfamily (Fig. 1), few clear biogeographic patterns can be discerned. The sister-species *D. viduata* and *D. autumnalis* both occur (at least in part) in South America, and perhaps can be characterized as sharing an "Atlantic" distribution. The remaining six species of *Dendrocygna,* with the exception of the West Indian *D. arborea,* share variably overlapping distributions in India, Indonesia, New Guinea, and Australia. Within this larger clade, the sister-species *D. arcuata* and *D. javanica* occupy virtually parapatric distributions, being sympatric only in Java and southern Borneo.

Biogeography and Perceived Relationships. — In light of the antiquity of the Dendrocygninae, the vagility of most waterfowl, and evidence for dispersal-related partitioning of lineages in *Dendrocygna* and other Anseriformes, assumptions concerning vicariance events and likely distributions of suspected sister-species in the group may be misleading. Unfortunately, geographical distributions have been used to infer phylogenetic relationships among selected species of *Dendrocygna,* and these interpretations have been made in sharply contradictory ways. For example, Johnsgard (1978:15) cited "their nonoverlapping distributions" as evidence supporting a close relationship between *D. bicolor* and *D. arcuata,* apparently assuming that sister-species should be allopatric. However, Johnsgard (1978:17) later judged that *D. javanica* probably had "somewhat closer affinities" with *D. arcuata* than with *D. bicolor* in part because of the close proximity of the distributional ranges of *D. javanica* and *D. arcuata.*

Tropical Habitats and Anseriform Origins. — The geographical distributions of the basal lineages of Anseriformes (e.g., Anhimidae, *Anseranas, Cnemiornis, Cereopsis, Coscoroba,* and *Stictonetta*), as well as the southern distributions of most members of the Dendrocygninae, indicate a southern-hemispheric origin of the Anseriformes (Livezey, 1986, 1989). Northern hemisphere distributions of fossil species related to the Dendrocygninae, however, necessitate caution in the narrower hypothesis of southern-hemispheric origins of the Dendrocygninae (Livezey and Martin, 1988). The confinement of the Dendrocygninae to tropical and sub-

tropical zones (Weller, 1964c), together with the tropical habitats of the Anhimidae and *Anseranas*, suggest the additional hypothesis that early Anseriformes were not only southern but tropical in distribution (Murton and Kear, 1975). Support for this idea must await a critical phylogenetic analysis of several northern-hemispheric fossils considered by some to represent basal Anseriformes or transitional forms related to the Anseriformes, including *Romainvillia, Paranyroca, Presbyornis,* and as yet undescribed, screamer-like birds from the western United States (Brodkorb, 1964; Howard, 1964; Livezey, 1986; Olson and Feduccia, 1980; P. Houde, in preparation).

Acknowledgments

Literature Cited

Baumel, J. J. 1979. Osteologia. Pp. 53–122, *in* Nomina Anatomica Avium (J. J. Baumel, A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans, eds.), Academic Press, London, xxv + 637 pp.
Baumel, J. J., and L. M. Witmer. 1993. Osteologia. Pp. 45–132, *in* Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd Edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, eds.), Publication Number 23, Nuttall Ornithological Club, Cambridge, Massachusetts, xxiv + 779 pp.
Boetticher, H., von. 1942. Über die Einteilung der Familie der Entenvögel (Anatidae) in Unterfamilien und Sektionen. Zoologischer Anzeiger, 140:37–48.
———. 1952. Gänse- und Entenvögel aus aller Welt. Geest and Portig K.-G., Leipzig, 95 pp.
Bolen, E. G., and M. K. Rylander. 1974. Foot adaptations in four species of whistling-duck *Dendrocygna*. Wildfowl, 25:81–83.
———. 1983. Whistling-ducks: Zoogeography, ecology, anatomy. Texas Tech University Museum Special Publication, 20:1–67.
Brodkorb, P. 1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). Bulletin of the Florida State Museum (Biological Science), 8:195–335.
Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior: A research program in comparative biology. University of Chicago Press, Chicago, xii + 434 pp.
Brush, A. H. 1976. Waterfowl feather proteins: Analysis of use in taxonomic studies. Journal of Zoology (London), 179:467–498.
Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187, *in* Current Ornithology, Volume 1 (R. F. Johnston, ed.), Plenum Press, New York, xvi + 425 pp.
———. 1988. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59, *in* Speciation and Its Consequences (D. Otte and J. A. Endler, eds.), Sinauer Associates, Sunderland, Massachusetts, xiii + 679 pp.
Delacour, J. 1954. The Waterfowl of the World, Volume 1. Country Life, London, 284 pp.
———. 1959. The Waterfowl of the World, Volume 3. Country Life, London, 270 pp.
———. 1964. Corrections and additions. Pp. 327–354, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. Wilson Bulletin, 57:3–55.

EADIE, J. McA., F. P. KEHOE, AND T. D. NUDDS. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: A review of hypotheses. Canadian Journal of Zoology, 66:1709–1721.

EYTON, T. C. 1838. A Monograph on the Anatidae, or Duck Tribe. Longmans, London, x + 178 pp.

FAITH, D. P. 1989. Homoplasy as pattern: Multivariate analysis of morphological convergence in anseriforms. Cladistics, 5:235–258.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution, 39:783–791.

FRITH, H. J. 1967. Waterfowl in Australia. East–West Center Press, Honolulu, xxi + 328 pp.

HARVEY, P. H., AND M. D. PAGEL. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, viii + 239 pp.

HOWARD, H. 1964. Fossil Anseriformes. Pp. 233–326, in The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

HOYO, J., DEL, A. ELLIOTT, AND J. SARGATAL (EDS.). 1992. Handbook of the Birds of the World, Volume 1. Lynx Editions, Barcelona, 696 pp.

HUMPHREY, P. S., AND G. A. CLARK, JR. 1964. The anatomy of waterfowl. Pp. 167–232, in The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

JACOB, J. 1982. Integumentlipide-ihre chemische Struktur und ihre Bedeutung als systematisches Merkmal in der Zoologie. Funktionelle Biologie und Medizin, 1:83–90.

JACOB, J., AND A. GLASER. 1975. Chemotaxonomy of Anseriformes. Biochemical Systematics and Ecology, 2:215–220.

JOHNSGARD, P. A. 1960a. Comparative behavior of the Anatidae and its evolutionary implications. Wildfowl, 11:31–45.

———. 1960b. Hybridization in the Anatidae and its taxonomic implications. Condor, 62:25–33.

———. 1961a. The taxonomy of the Anatidae—A behavioural analysis. Ibis, 103:71–85.

———. 1961b. Tracheal anatomy of the Anatidae and its taxonomic significance. Wildfowl, 12:58–69.

———. 1962. Evolutionary trends in the behaviour and morphology of the Anatidae. Wildfowl, 13:130–148.

———. 1963. Behavioral isolating mechanisms in the family Anatidae. Pp. 531–543, in Proceedings XIII International Ornithological Congress, Volume 1 (C. G. Sibley, ed.), American Ornithologists' Union, Washington, D.C., xiv + 610 pp.

———. 1965. Handbook of Waterfowl Behavior. Constable, London, xiv + 378 pp.

———. 1967. Observations on the behaviour and relationships of the White-backed Duck and the stiff-tailed ducks. Wildfowl, 18:98–107.

———. 1978. Ducks, Geese, and Swans of the World. University of Nebraska Press, Lincoln, xxiii + 404 pp.

———. 1979. Order Anseriformes. Pp. 425–506, in Checklist of Birds of the World, Volume 1, 2nd Edition (E. Mayr and C. W. Cottrell, eds.), Museum of Comparative Zoology, Cambridge, Massachusetts, xvii + 547 pp.

KEAR, J. 1967. Notes on the eggs and downy young of Thalassornis leuconotus. Ostrich, 38:227–229.

———. 1970. The adaptive radiation of parental care in waterfowl. Pp. 357–392, in Social Behaviour in Birds and Mammals (J. H. Crook, ed.), Academic Press, New York, xl + 492 pp.

KING, A. S. 1989. Functional anatomy of the syrinx. Pp. 105–192, in Form and Function in Birds, Volume 4 (A. S. King and J. McLelland, eds.), Academic Press, London, xiii + 591 pp.

LIVEZEY, B. C. 1986. A phylogenetic analysis of Recent anseriform genera using morphological characters. Auk, 103:737–754.

———. 1989. Phylogenetic relationships of several subfossil Anseriformes of New Zealand. University of Kansas, Museum of Natural History Occasional Papers, 128:1–25.

———. 1991. A phylogenetic analysis and classification of Recent dabbling ducks (Tribe Anatini) based on comparative morphology. Auk, 108:471–507.

———. In press a. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor.

———. In press b. Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). Wilson Bulletin.

LIVEZEY, B. C., AND P. S. HUMPHREY. 1984. Sexual dimorphism in continental steamer-ducks. Condor, 86:368–377.

LIVEZEY, B. C., AND L. D. MARTIN. 1988. The systematic position of the Miocene anatid Anas[?] blanchardi Milne-Edwards. Journal of Vertebrate Paleontology, 8:196–211.

LUCAS, A. M. 1979. Integumentum commune. Pp. 7–51, *in* Nomina Anatomica Avium (J. J. Baumel, A. S. King, A M. Lucas, J. E. Breazile, and H. E. Evans, eds.), Academic Press, London, xxv + 637 pp.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Version 3. Sinauer Associates, Sunderland, Massachusetts, xi + 398 pp.

MADGE, S. C., AND H. BURN. 1988. Waterfowl: An Identification Guide to the Ducks, Geese and Swans of the World. Houghton Mifflin, Boston, 298 pp.

MADSEN, C. S., K. P. MCHUGH, AND S. R. DE KLOET. 1988. A partial classification of waterfowl (Anatidae) based on single-copy DNA. Auk, 105:452–459.

MARCHANT, S., AND P. J. HIGGINS (COORDS.). 1990. Handbook of Australian, New Zealand and Antarctic Birds, Volume 1, Part B. Oxford University Press, Melbourne, pp. 737–1400.

MCKITRICK, M. C., AND R. M. ZINK. 1988. Species concepts in ornithology. Condor, 90:1–14.

MCNEIL, R., P. DRAPEAU, AND J. D. GOSS-CUSTARD. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. Biological Review, 67:381–419.

MILLER, A. H. 1944. An avifauna from the lower Miocene of South Dakota. University of California Publications, Bulletin of the Department of Geological Sciences, 27:85–100.

MURTON, R. K., AND J. KEAR. 1975. The role of daylength in regulating the breeding seasons and distributions of wildfowl. Pp. 337–357, *in* Light as an Ecological Factor: II (G. C. Evans, R. Bainbridge, and O. Rackham, eds.), Blackwell Scientific Publications, Oxford, xiv + 616 pp.

NELSON, C. J. 1993. The Downy Waterfowl of North America. Delta Station Press, Deerfield, Illinois, xx + 302 pp.

NUMACHI, K., M. WATADA, R. KAKIZAWA, N. KURODA, AND S. UTIDA. 1983. Evolutionary genetics of the Anatidae. Tori, 32:63–74.

OLSON, S. L., AND A. FEDUCCIA. 1980. *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). Smithsonian Contributions to Zoology, 323:1–24.

PARKES, K. C. 1978. A guide to forming and capitalizing compound names of birds in English. Auk, 95:324–326.

PETERS, J. L. 1931. Check-list of Birds of the World, Volume 1. Harvard University Press, Cambridge, Massachusetts, xviii + 345 pp.

PHILLIPS, J. C. 1922. A Natural History of the Ducks, Volume 1. Houghton Mifflin, Boston, 264 pp.

RAIKOW, R. J. 1971. The osteology and taxonomic position of the White-backed Duck, *Thalassornis leuconotus*. Wilson Bulletin, 83:270–277.

ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. Auk, 105:161–176.

ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. Canadian Journal of Zoology, 67:239–253.

RYLANDER, M. K., AND E. G. BOLEN. 1970. Ecological and anatomical adaptations of North American tree ducks. Auk, 87:72–90.

RYLANDER, M. K., E. G. BOLEN, AND R. E. MCCAMANT. 1980. Evidence of incubation patches in whistling-ducks. Southwestern Naturalist, 25:123–128.

SALVADORI, T. 1895. Catalogue of the Chenomorphae (Palamedeae, Phoenicopteri, Anseres), Crypturi and Ratitae in the Collection of the British Museum. British Museum, London, xv + 636 pp.

SANDERSON, M. J. 1989. Confidence limits on phylogenies: The bootstrap revisited. Cladistics, 5:113–129.

SCHERER, S., AND T. HILSBERG. 1982. Hybridisierung und Verwandtschaftsgrade innerhalb der Anatidae—eine systematische und evolutionstheroetische Betrachtung. Journal für Ornithologie, 123: 357–380.

SCHERER, S., AND C. SONTAG. 1986. Zur molekularen Taxonomie und Evolution der Anatidae. Zeitschrift für Zoologische Systematik und Evolutionforschung, 24:1–19.

SCHIØLER, E. L. 1926. Danmarks Fugle, Volume 2. Nordisk Forlag, Kobenhavn, 338 pp.

SCHÖNWETTER, M. 1961. Handbuch der Oologie, Part 3. Akademie Verlag, Berlin, pp. 129–192.

SCLATER, P. L. 1864. Note on the geographical distribution of the ducks of the genus *Dendrocygna*. Proceedings of the Zoological Society of London, 1864:299–301.

SCOTT, D. K., AND T. H. CLUTTON-BROCK. 1989. Mating systems, parasites and plumage dimorphism in waterfowl. Behavioral Ecology and Sociobiology, 26:261–273.

SHUFELDT, R. W. 1909. Osteology of Birds. New York State Museum Bulletin 130, State University of New York, Albany, 381 pp.

———. 1914. Contributions to the study of the "tree-ducks" of the genus *Dendrocygna*. Zoologische Jahrbücher (Systematik, Geographie und Biologie der Tiere), 38:1–70.

SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor, 59:166–191.

Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and Classification of Birds: A Study in Molecular Evolution. Yale University Press, New Haven, Connecticut, xxiii + 976 pp.

Sibley, C. G., and B. L. Monroe, Jr. 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut, xxiv + 1111 pp.

Sibley, C. G., J. E. Ahlquist, and B. L. Monroe, Jr. 1988. A classification of the living birds of the world based on DNA–DNA hybridization studies. Auk, 105:409–423.

Siegfried, W. R. 1973. Morphology and ecology of the southern African whistling ducks (*Dendrocygna*). Auk, 90:198–201.

Sigurjónsdóttir, H. 1981. The evolution of sexual size dimorphism in gamebirds, waterfowl and raptors. Ornis Scandinavica, 12:249–260.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1, March 1993. Laboratory of Molecular Systematics, Smithsonian Institution, Washington, D.C., vi + 257 pp.

Verheyen, R. 1953. Dijdrage tot de osteologie en de systematiek der Anseriformes. Gerfaut, 43: 373–456.

Weller, M. W. 1964a. General habits. Pp. 15–34, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

———. 1964b. Ecology. Pp. 80–107, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

———. 1964c. The reproductive cycle. Pp. 35–79, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

———. 1964d. Distribution and species relationships. Pp. 108–120, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, 364 pp.

Wetmore, A. 1924. Fossil birds from southeastern Arizona. Proceedings of the United States National Museum, 64:1–18.

Wiley, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. J. Wiley and Sons, New York, xv + 439 pp.

Wolters, H. E. 1976. Die Vogelarten der Erde, Part 2. Paul Parey, Hamburg and Berlin, pp. 81–160.

Womack, S. M., M. K. Rylander, and E. G. Bolen. 1977. The structure of the retina in four species of whistling-ducks, *Dendrocygna*. Texas Journal of Science, 29:141–142.

Woolfenden, G. E. 1961. Postcranial osteology of the waterfowl. Florida State Museum Bulletin (Biological Science), 6:1–129.

Appendix 1

Character Descriptions

Characters analyzed as unordered unless indicated otherwise. Plesiomorphous state is designated "a" unless indicated otherwise in boldface. Osteological characters based on those of Livezey (1986) are identified parenthetically. Consistency indices (CI) for characters in the shortest tree (Fig. 1, 2) follow each description. Asterisks indicate characters of undetermined polarity. Anatomical nomenclature follows Baumel (1979), Lucas (1979), and Baumel and Witmer (1993).

Skeleton

1. Os prefrontale, processus orbitalis: (a) terminates only slightly posterior to anterior margin of orbit; (b) extends posteriorly, typically fused to processus postorbitalis of squamosal by tendo ossificans, forming arcus suborbitalis (Fig. 5; Shufeldt, 1914; Schiøler, 1926). (Livezey, 1986:character 10, revised.) CI = 1.00.

2. Sternum, corpus sterni, facies visceralis sterni, foramen pneumaticum: (a) open, ovoid; (b) absent. (Livezey, 1986:character 78, revised.) CI = 1.00.

3. Humerus, extremitas distalis humeri, tuberculum supracondylare ventrale: (a) prominent, coplanar with corpus humeri, facies cranialis; (b) prominent, angled distally. (Livezey, 1986:character 26.) CI = 1.00.

4. Humerus, extremitas proximalis humeri, incisura capitis: (a) short, oriented
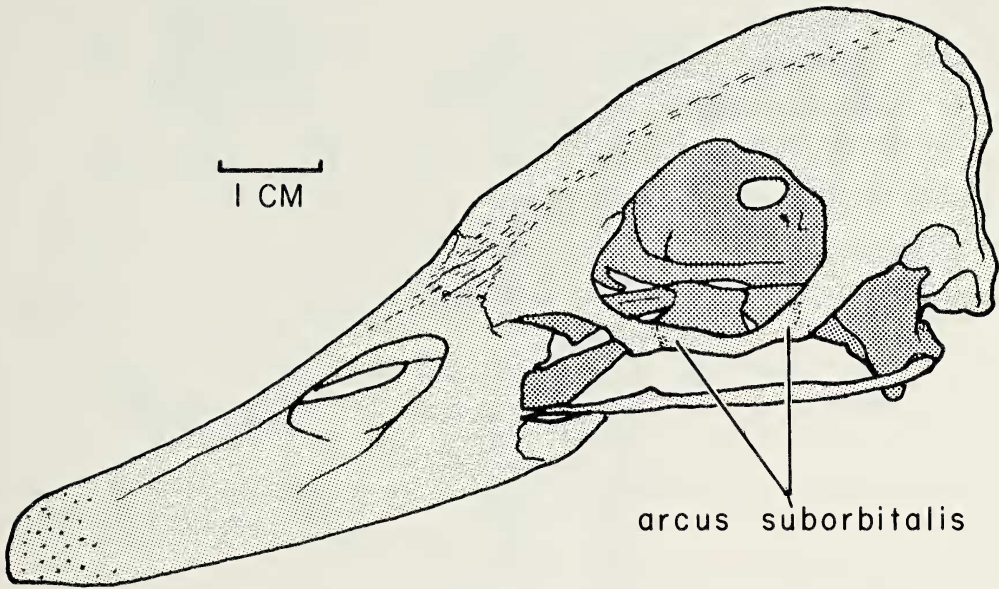
Fig. 5.—Dorsolateral view of cranium and maxilla of *Dendrocygna autumnalis* (KUMNH 37725), showing generic synapomorphy of arcus suborbitalis (character 1).

proximodistally; (b) long, extended ventrally, undercutting caput humeri. (Livezey, 1986:character 23.) CI = 1.00.

5. Humerus, extremitas proximalis humeri, tuberculum ventrale: (a) proximal, exposing fossa pneumotricipitalis in caudal view; (b) distal, largely concealing fossa pneumotricipitalis in caudal view. (Livezey, 1986:character 27.) CI = 1.00.

6. Humerus, extremitas proximalis humeri, fossa pneumotricipitalis, foramen pneumaticum: (a) present, highly pneumatic; (b) completely occluded. (Livezey, 1986:character 28, revised.) CI = 1.00.

7. Humerus, extremitas proximalis humeri, tuberculum dorsale: (a) not prominent, impressio m. supracoracoidei sloping with crista pectoralis, facies caudalis; (b) prominent, impressio m. supracoracoidei raised from crista pectoralis, facies caudalis by "buttress." (Livezey, 1986:character 32, revised.) CI = 1.00.

8. Pelvis, ala ilii, medial fusion with synsacrum, crista dorsalis, relative to acetabula: (a) cranial; (b) opposite. (Livezey, 1986:character 119, revised.) CI = 1.00.

9. Femur, extremitas proximalis femoris, trochanter femoris, cranial prominence relative to craniocaudal depth of caput femoris: (a) substantially greater; (b) equal. (Livezey, 1986:character 52.) CI = 1.00.

10. Femur, corpus femoris, craniocaudal curvature (lateral perspective): (a) absent; (b) moderate. (Livezey, 1986:character 55, revised.) CI = 1.00.

11. Tibiotarsus, extremitas distalis tibiotarsi, condylus medialis, cranial prominence relative to condylus lateralis: (a) greater; (b) equal. (Livezey, 1986:character 64.) CI = 1.00.

12. Tibiotarsus, extremitas proximalis tibiotarsi, crista cnemialis cranialis, distinct ridge continuing on corpus tibiotarsis, facies cranialis distal to terminus of crista fibularis: (a) absent; (b) present. (Livezey, 1986:character 65.) CI = 1.00.
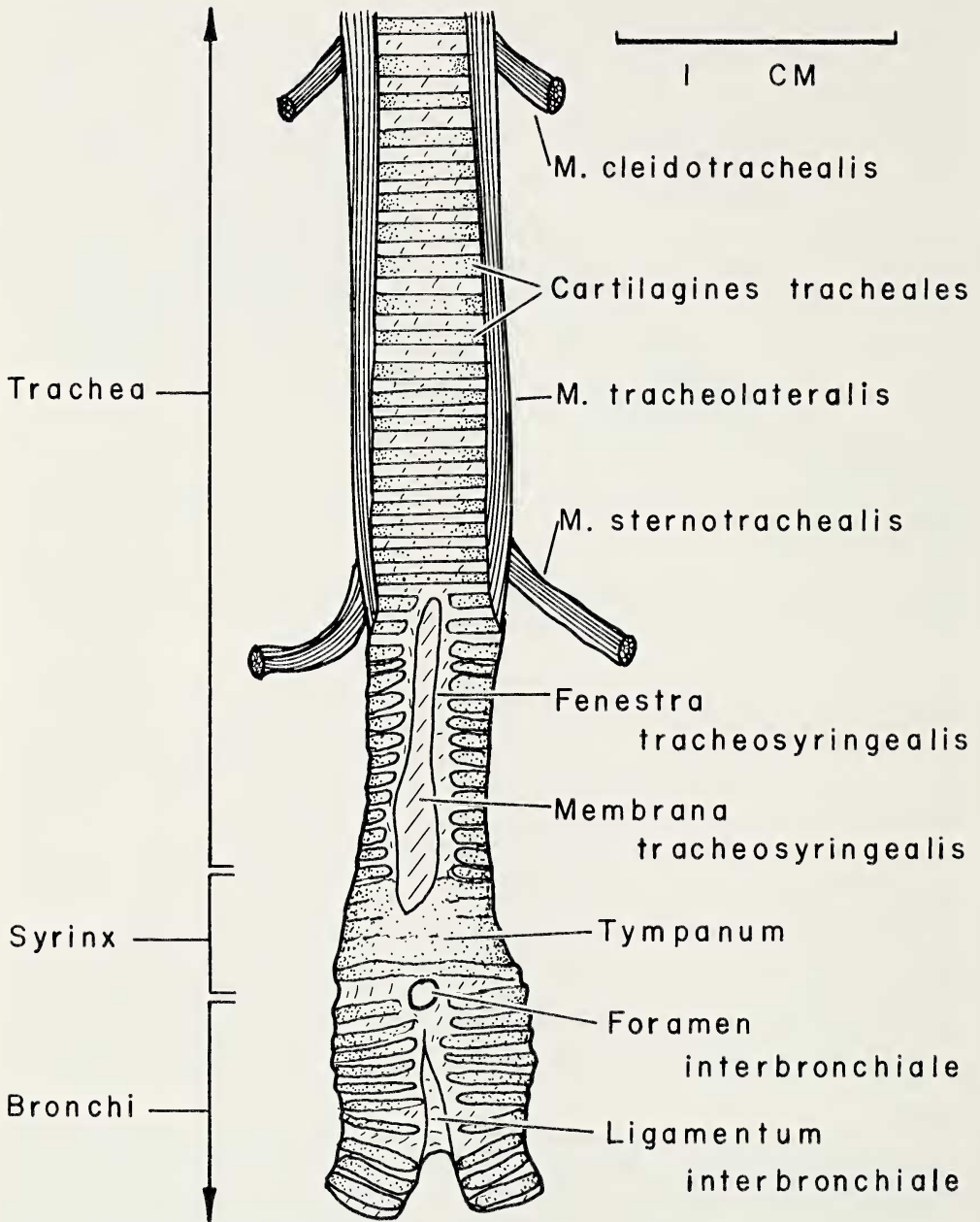
Fig. 6.—Trachea of *Dendrocygna viduata*, female (USNM 227118), ventral view of caudal segment, showing generic synapomorphy of fenestra tracheosyringealis (character 14).

13. Tarsometatarsus, corpus tarsometatarsi, facies dorsalis, margo medialis, dorsal prominence relative to margo lateralis: (a) essentially equal; (b) significantly less, associated with pronounced torsion of corpus around long axis. (Livezey, 1986:character 75, revised.) CI = 1.00.
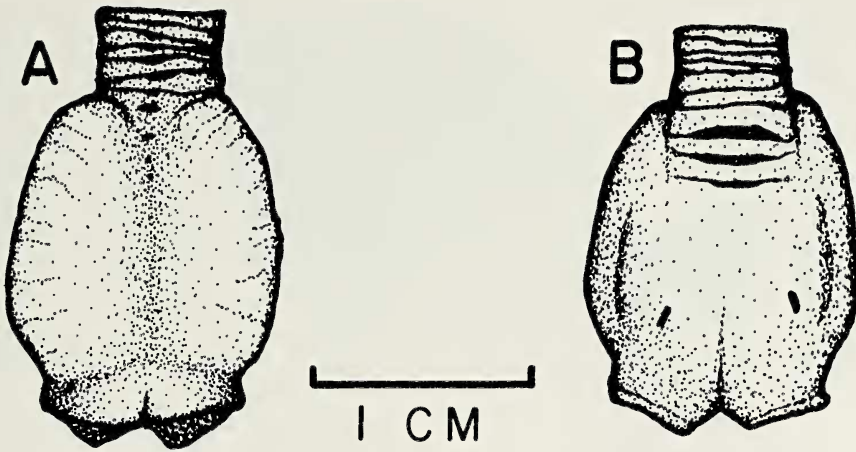
Fig. 7.—Symmetrically enlarged bulla syringealis (character 15) of *Dendrocygna arcuata,* male (KUMNH 85349): A—dorsal view; B—ventral view.

Trachea and Syrinx

14. Trachea, fenestra et membrana tracheosyringealis ventralis (females): (a) absent; (b) present (Fig. 6). CI = 1.00.

15. Syrinx, tympanum, symmetrical inflation without fenestrae (males): (a) absent; (b) present (Fig. 7). (Livezey, 1986:character 6, revised.) CI = 1.00.

Natal Plumage (*Fig. 8, 9*)

(Dusky breast band intraspecifically variable, excluded [Fig. 8].)

16. Ground color: (a) yellow; (b) whitish. CI = 1.00.

17. Scapular and rump spots: (a) present; (b) absent. CI = 1.00.

18. Scapular and rump spots: (a) separate; (b) confluent; (x) noncomparable. CI = 0.50.

19. Pale suborbital stripe (ordered): (a) terminating at dark nape; (b) ventrally displaced by broad orbital stripe, separated dorsally by narrow nuchal stripe; (c) meeting across nape. CI = 1.00. (State for *Thalassornis* [Fig. 9] problematic; see character 23 and text.)

20. Pale supraorbital stripe: (a) broad; (b) narrow or absent. CI = 0.50.

21. General dorsal color: (a) sharply darker than ventrum; (b) pale. CI = 1.00.

22. Contrastingly dusky thighs: (a) absent; (b) present. CI = 1.00.

23. Broad dark stripe from base of nape to auricular region: (a) absent; (b) present. CI = 1.00. (State for *Thalassornis* [Fig. 9] problematic; see character 19 and text.)

Definitive Plumage and Soft Parts

24. Leg, ground color: (a) black or gray (*guttata* with reddish mottling); (b) flesh (in juveniles and adults); (c) deep pink (adults only). CI = 1.00.

25. Sides and flanks: (a) feathers not having white medial stripe and dark margins; (b) feathers with white medial stripe and dark margins (tending to tri-
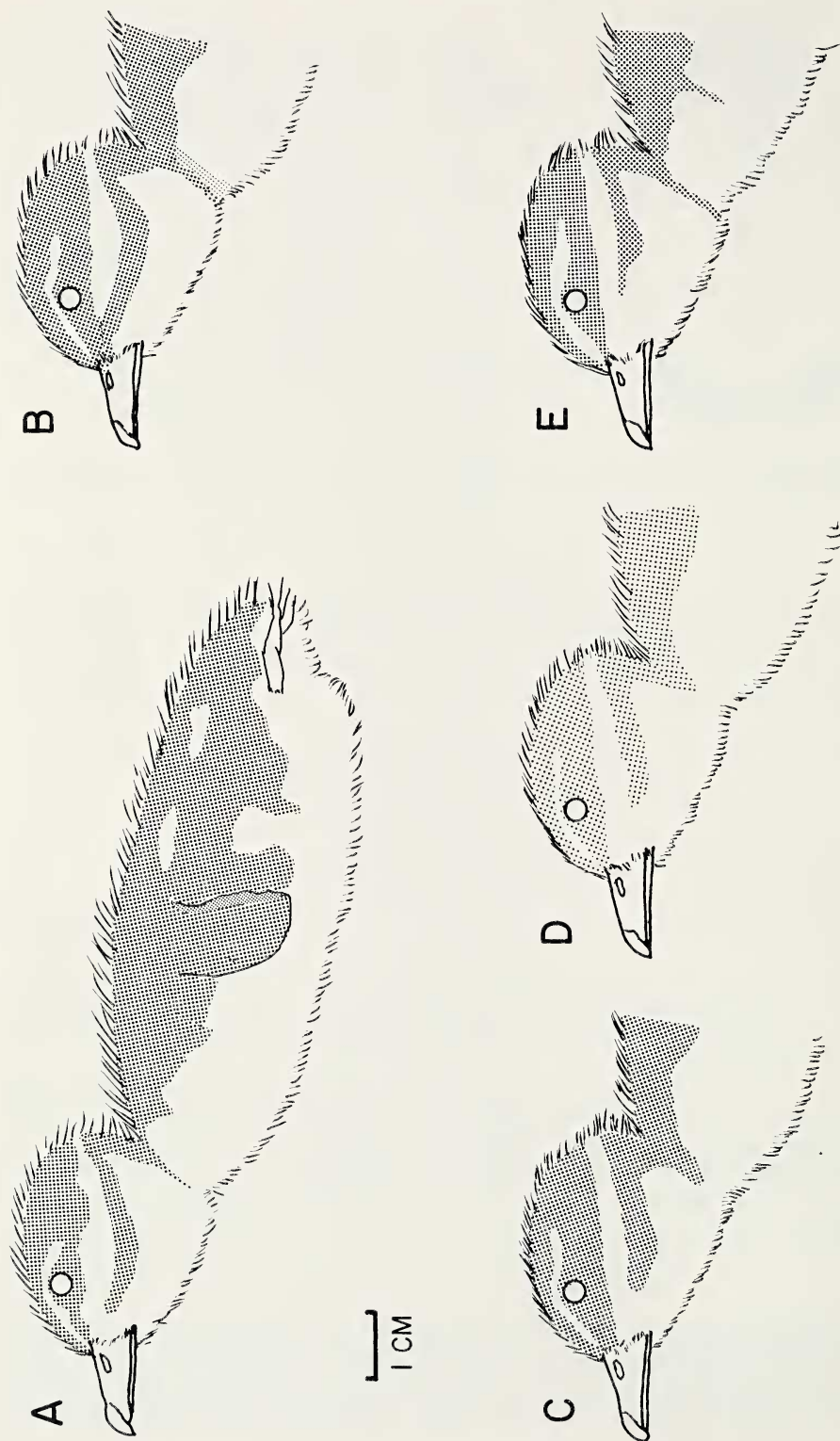
Fig. 8.—Natal plumages of selected *Dendrocygna*, lateral views (see characters 16–23): A—*D. arborea* (FMNH 14699), showing dorsal spotting; B—*D. arborea* (FMNH 14698), illustrating variation in pectoral band; C—*D. autumnalis* (AMNH 348817); D—*D. bicolor* (AMNH 79641); E—*D. javanica* (UMMZ 228575).
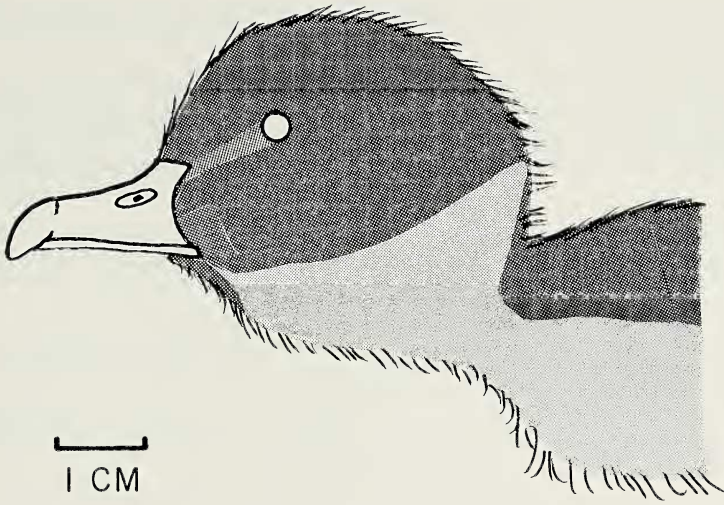
Fig. 9.—Natal pattern of *Thalassornis leuconotus* (AMNH 410826), lateral view (see characters 16–23).

lobate shape in *arborea*); (c) feathers with three white, semielliptical medial spots. CI = 1.00.

26. Wing, upper lesser coverts: (a) not chestnut; (b) chestnut, extensive; (c) chestnut, comparatively restricted. CI = 1.00.

27. Contrasting rump patches or band: (a) absent; (b) present, spotted, variably complete; (c) present, broad, complete; (d) present, medially divided. CI = 1.00.

28. Feathers of sides and flanks, chestnut ventral margins: (a) absent; (b) present. CI = 0.50.

29. Lower breast and belly, distinct tawny color: (a) absent; (b) present. CI = 1.00.

30. Breast, golden-olive cast, variably distinct from ventrum: (a) absent; (b) present. CI = 1.00.

31. Belly, flanks, undertail coverts: (a) not black; (b) black throughout, variably mottled with white (*autumnalis*) or black medially (*viduata*). CI = 1.00.

32. Upper back, chestnut color: (a) absent; (b) present (nominate *autumnalis* comparatively extensive). CI = 1.00.

33. Blurred, whitish marks (typically two) on feathers of lower neck, breast: (a) absent; (b) present. CI = 1.00.

34. Base of bill: (a) colored like rest of bill; (b) contrastingly flesh-colored. CI = 1.00.

35. Broad, black-and-chestnut barring on belly, sides: (a) absent; (b) present. CI = 1.00.

36. Entirely fulvous ventrum: (a) absent; (b) present. CI = 1.00.

37. Blackish spotting on breast, upper belly: (a) absent; (b) present. CI = 1.00.

38. Rump band (if present): (a) white; (b) chestnut. CI = 1.00.

39. Contrastingly white crown, face, throat: (a) absent; (b) present. CI = 1.00.

40. Ground color of bill: (a) dark gray; (b) pink (with grayish mottling); (c) bright red. CI = 1.00.

41. Greater upper coverts of primary and secondary remiges, contrasting pale stripe: (a) absent; (b) present, white (*autumnalis*) or pale gray (*arborea*). CI = 0.50.

42. Dorsal wing coverts, sharp black spotting: (a) absent; (b) present. CI = 1.00.

43. Distinct wash of chestnut across lower neck: (a) absent; (b) present. CI = 1.00.

44. Pale subterminal band of maxilla: (a) absent; (b) present. CI = 1.00.

45. Dark craniocaudal striations on side of neck: (a) absent; (b) present. CI = 1.00.

46. Iris color: (a) dark brown; (b) yellow. CI = 1.00.

47. Contrastingly pale eye ring: (a) absent; (b) present, inconspicuous, buffy; (c) present, conspicuous, white. CI = 1.00.

48. Dark nuchal stripe: (a) absent; (b) present from crown to mantle (comparatively spotted in *Thalassornis*); (c) present, but markedly narrowing caudally (*arcuata*) or truncated at occiput (*javanica*). CI = 1.00.

49. Nuchal stripe (if present), caudal segment: (a) distinctly darker than mantle; (b) not distinctly darker than mantle. CI = 0.33.

50. Dark breast band: (a) absent; (b) present, spotted and diffuse; (c) present, distinct. CI = 1.00.

51. Feathers of dorsum with pale terminal margins: (a) absent; (b) present (*Thalassornis* also having subterminal brown bar; *Dendrocygna autumnalis* weak). CI = 1.00.

52. Undertail coverts, ground color*: (a) white; (b) brownish; (c) black. CI = 0.67.

53. Black, bilateral spotting on undertail coverts: (a) absent; (b) present. CI = 0.50.

54. Face, ground color: (a) variably brownish; (b) distinctly gray (comparatively restricted in *arborea*); (x) noncomparable. CI = 0.50.

55. Sides and flanks, narrow black-and-white barring: (a) absent; (b) present. CI = 1.00.

56. Undertail coverts, broad, black transverse barring: (a) absent; (b) present. Note—In *Thalassornis,* feathers interpreted as dark brown with white bars. CI = 1.00.

57. Elongated plumes of flanks (if present), tips: (a) rounded; (b) pointed. CI = 0.50.

58. Plumage of body, feathers dark brown transversely marked with 2–3 variably broad, sometimes medially incomplete bars of buff: (a) absent; (b) present. CI = 1.00.

59. Mentum, contrastingly black: (a) absent; (b) present. CI = 1.00.

60. Small, lateral white patches at sides of bill: (a) absent; (b) present. CI = 1.00.

61. Lower back, contrasting white patch: (a) absent; (b) present. CI = 1.00.

62. Rectrices, shape: (a) broad, comparatively rounded; (b) narrow, pointed. CI = 1.00.

63. Hallux, cutaneous lobation: (a) absent; (b) present. CI = 1.00.

64. Face, orange-buff coloration with black spotting: (a) absent; (b) present. CI = 1.00.

65. Dertrum, broad, thick, and strongly hooked: (a) absent; (b) present. CI = 1.00.

66. Webbing between pedal digits: (a) complete; (b) moderately incised. CI = 1.00.

67. Claws on pedal digits: (a) comparatively short; (b) comparatively long. CI = 0.50.

68. Hallux, relative length: (a) not great, hallux barely extending to bases of other digits; (b) great, hallux extending beyond bases of other digits (*javanica* comparatively short). CI = 1.00.

Mapped Attributes (Primitive States in Boldface)

A. Mean body mass (g; ordered): (a) <600; (b) 600–800; (c) 800–1200; **(d) >1200**.

B. Mean clutch size (ordered): **(a) <8**; (b) 8–10; (c) >10.

C. Mean egg mass (g; ordered): (a) <40; (b) 40–50; (c) 50–100; **(d) >100**.

D. Relative clutch mass (percentage of mean female body mass; ordered): **(a) 40–50**; (b) 50–60; (c) 60–70; (d) 70–80; (e) >80.

E. Preferred nest site (ordered): **(a) terrestrial**; (b) variable; (c) cavity.

F. Perching habit: **(a) developed**; (b) not developed.

G. Diving habit (ordered): **(a) absent**; (b) moderate; (c) pronounced.

H. Period of activity (ordered): **(a) diurnal**; (b) crepuscular; (c) nocturnal.

APPENDIX 2

Data Matrix

Matrix of 68 morphological characters (described in Appendix 1) used in the phylogenetic analysis of the Dendrocygninae, rooted using a hypothetical ancestor, followed by eight attributes mapped *a posteriori* (lettered A–H). Skeletal characters are labelled "s1" to "s13," tracheal characters "t1" to "t2," natal characters "n1" to "n8," and those of definitive integument "d1" to "d45." States are coded as lowercase letters, and question marks signify undetermined states.

		1 s1	2 s2	3 s3	4 s4	5 s5	6 s6	7 s7	8 s8	9 s9	10 s10	11 s11	12 s12	13 s13	14 t1	15 t2	16 n1	17 n2	18 n3	19 n4
1	Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2	*T. leuconotus*	a	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	b
3	*D. viduata*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	a	a	c
4	*D. autumnalis*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	a	a	c
5	*D. eytoni*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	b	c
6	*D. bicolor*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	a	c
7	*D. guttata*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	b	c
8	*D. arborea*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	a	c
9	*D. arcuata*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	b	?	c
10	*D. javanica*	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	a	c

		20 n5	21 n6	22 n7	23 n8	24 d1	25 d2	26 d3	27 d4	28 d5	29 d6	30 d7	31 d8	32 d9	33 d10	34 d11	35 d12	36 d13	37 d14	38 d15
1	Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2	*T. leuconotus*	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3	*D. viduata*	a	a	a	b	a	a	c	a	a	a	a	b	b	a	a	a	a	a	a
4	*D. autumnalis*	a	a	a	b	c	a	a	a	a	a	a	c	b	a	a	a	a	a	a
5	*D. eytoni*	a	a	a	b	b	b	a	c	a	b	b	a	a	a	a	b	a	a	a
6	*D. bicolor*	b	b	a	b	a	b	a	c	b	b	b	a	a	a	a	a	b	a	a
7	*D. guttata*	a	a	a	b	a	c	a	b	a	a	b	a	a	b	b	a	a	a	a
8	*D. arborea*	a	a	a	b	a	b	a	a	a	a	b	a	a	b	a	a	a	a	a
9	*D. arcuata*	a	a	b	b	a	b	b	d	b	b	b	a	a	a	a	a	a	b	a
10	*D. javanica*	a	a	a	b	a	b	b	d	a	b	b	a	a	a	a	a	a	a	b

		39 d16	40 d17	41 d18	42 d19	43 d20	44 d21	45 d22	46 d23	47 d24	48 d25	49 d26	50 d27	51 d28	52 d29	53 d30	54 d31	55 d32	56 d33	57 d34
1	Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	?	a	a	a	a	a
2	*T. leuconotus*	a	a	a	a	a	a	a	a	a	b	b	a	b	b	a	a	a	a	a
3	*D. viduata*	b	a	a	a	b	b	a	a	a	b	a	c	b	c	a	?	b	a	a
4	*D. autumnalis*	a	c	b	a	b	a	a	a	c	b	a	c	b	a	b	b	a	a	a
5	*D. eytoni*	a	b	a	a	a	a	a	b	a	b	b	a	b	a	a	a	a	a	b
6	*D. bicolor*	a	a	a	a	a	a	b	a	a	b	a	a	b	a	a	a	a	a	b
7	*D. guttata*	a	a	a	a	a	a	a	a	a	b	a	b	b	a	b	b	a	b	a
8	*D. arborea*	a	a	b	b	a	a	a	a	a	b	a	b	b	a	b	b	a	a	a
9	*D. arcuata*	a	a	a	a	a	a	a	a	a	c	a	a	b	b	a	a	a	a	b
10	*D. javanica*	a	a	a	a	a	a	a	b	c	b	a	b	a	b	a	a	a	a	a

		58 d35	59 d36	60 d37	61 d38	62 d39	63 d40	64 d41	65 d42	66 d43	67 d44	68 d45	69 A	70 B	71 C	72 D	73 E	74 F	75 G	76 H
1	Ancestor	a	a	a	a	a	a	a	a	a	a	a	d	a	d	a	a	a	a	a
2	*T. leuconotus*	b	b	b	b	b	b	b	b	a	a	a	b	b	c	e	a	b	c	b
3	*D. viduata*	a	a	a	a	a	a	a	a	b	b	b	b	b	a	c	a	b	b	c
4	*D. autumnalis*	a	a	a	a	a	a	a	a	b	b	b	c	c	b	d	b	a	a	c
5	*D. eytoni*	a	a	a	a	a	a	a	a	b	b	b	b	c	a	a	a	b	a	c
6	*D. bicolor*	a	a	a	a	a	a	a	a	b	b	b	b	b	b	d	a	b	a	c
7	*D. guttata*	a	a	a	a	a	a	a	a	b	b	b	b	c	b	b	c	a	?	b
8	*D. arborea*	a	a	a	a	a	a	a	a	b	b	b	c	b	b	a	b	a	a	c
9	*D. arcuata*	a	a	a	a	a	a	a	a	b	b	b	b	b	a	b	a	b	b	a
10	*D. javanica*	a	a	a	a	a	a	a	a	b	a	b	a	b	a	c	b	a	b	b

APPENDIX 3

Taxonomy of Dendrocygninae

Conventions for hyphenation and capitalization of English names follows Parkes (1978). Tribe Thalassornithini replaces Subfamily Thlassornithinae Livezey, 1989, an emendation of etymologically incorrect taxon Thalassorninae Livezey, 1986.

Order Anseriformes (Wagler, 1831).
  Suborder Anseres Wagler, 1831.
  Family Anatidae Vigors, 1825.

Subfamily Dendrocygninae Reichenbach, "1850".—Proto-ducks.
  Tribe Dendrocygnini Delacour and Mayr, 1945.—Whistling-ducks.
    Genus *Dendrocygna* Swainson, 1837.
      Subgenus *Lamprocygna* (> *Prosopocygna*) Boetticher, 1949.
        Dendrocygna viduata (Linnaeus, 1766).—White-faced Whistling-Duck.
        Dendrocygna autumnalis (Linnaeus, 1758).—Black-bellied Whistling-Duck.
      Subgenus *Dendrocygna* Swainson, 1837.
        Infragenus *Nesocygna* (> *Stagonocygna*) Boetticher, 1949.
        Dendrocygna guttata Schlegel, 1866.—Spotted Whistling-Duck.
        Dendrocygna arborea (Linnaeus, 1758).—West Indian Whistling-Duck.
      Infragenus *Dendrocygna* Swainson, 1837 (> *Leptotarsus* Eyton, 1838); *sedis mutabilis.*
        Dendrocygna arcuata (Horsfield, 1824).—Wandering Whistling-Duck.
        Dendrocygna javanica (Horsfield, 1821).—Lesser Whistling-Duck.
        Dendrocygna eytoni (Eyton, 1838).—Plumed Whistling-Duck.
        Dendrocygna bicolor (Vieillot, 1816).—Fulvous Whistling-Duck.
  Tribe Thalassornithini, new taxon.
  Genus *Thalassornis* Eyton, 1838.
        Thalassornis leuconotus Eyton, 1838.—White-backed Duck.